

**Intraspecific competition and winter sociality in
white-winged snowfinches (*Montifringilla nivalis*)**

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Summary

In winter in the mountains, foraging is challenging due to low availability of food, even for species adapted to cold environments. Forming social groups can then improve foraging efficiency but may also increase intraspecific competition. White-winged snowfinches (*Montifringilla nivalis*) use alpine habitats all year round and forage in groups during the winter season. Studies dealing with the social behaviour of this species or the competitive situation in their foraging groups are lacking. However, knowledge of the social behaviour would help to understand how snowfinches survive winter conditions at high elevations. Here we investigated how snowfinches interact at artificial feeding sites. Specifically, we were interested in how they cope with competition for food within flocks, how individuals differ in their social behaviour and how individual behaviour is linked to morphological characteristics and to getting access to food. We provided supplementary food at two identical food patches that we placed 6-8 meters apart from each other. We used video recordings to monitor how snowfinches distributed between the alternative patches and when agonistic interactions for food resources occurred. Further, we observed colour-ringed snowfinches within groups, to examine how they interact with conspecifics, how close they get to the most profitable positions on the feeding patch, and what beak colour and sex they have. We found that snowfinches in groups of up to 60 individuals preferentially chose the food patch where their group members were feeding instead of the other, unoccupied patch. Moreover, the number of agonistic interactions decreased with increasing group size. The individuals involved in more interactions foraged closer to the centre of the food patch and were mostly males. We also showed that individuals who initiated more agonistic interactions might have blacker beaks than their conspecifics. We suggest that snowfinches benefit more from foraging in groups in winter than they suffer from competition. Nevertheless, it seems that individuals differ in their competitive ability. The more aggressive birds may have better access to food. Their beak colour could act as a signal for aggressiveness or competitiveness in interactions at feeding sites.

1. Introduction

Reduced availability of food and low temperatures in winter, are challenging for most bird species living in temperate regions. Foraging needs to be efficient so that birds gain enough energy for keeping warm and escaping predators (Charnov 1976, McNamara et al. 1994). Even species adapted to cold environments may have lower chances of survival in winter (Nilson et al. 2020). A strategy to face these challenges is forming groups (Caraco et al. 1980). Social foraging is hypothesized to improve the finding of feeding sites (Newton 2008), to increase food intake (Barnard 1980), and to reduce predation risk (Sorato et al. 2012). Disadvantages for group members usually result from increased intraspecific competition (Milinski & Parker 1991). Competition was often reflected in an increase in agonistic interactions between group members and a resulting decrease in food intake (Goss-Custard & Durell 1988, Benkman 1997, Rose & Soole 2020). Joining a group always requires trading off advantages against disadvantages a group can have, depending on environmental circumstances (del Mar Delgado et al. 2021). How strong competition is, depends to a large extent on the amount and distribution of accessible resources (Slobodchikoff & Schultz 1988). The more limited and unevenly distributed the food resources, the stronger the competition between group members (Krause & Ruxton 2002).

Not all group members need to be equally affected by limitations in food supply or increased competition (Carrascal et al. 1988). Costs of grouping are likely to be higher for less competitive, subordinate individuals than for more competitive, dominant individuals (Ward and Webster 2016). It was shown that subordinates do not have the same access to food (Carrascal et al. 1989, Ficken et al. 1990, Francis et al. 2018) or sheltered places (Dostie et al. 2016) than dominants. Some studies also found increased mortality among subordinates (Desrochers et al. 1988, Schubert et al. 2008). Who is dominant or subordinate can depend on a variety of factors, such as sex (Smith 1980); body weight, size, age (Hermann 2017) or aggressiveness of an individual, as well as fighting experience (Favati et al. 2017).

Privileges of dominants can force subordinates to use alternative strategies to optimally benefit from groups (Gross 1996). For example, the use of defensive strategies by subordinates, while dominants

monopolize resources, could reduce conflicts in competitive situations (Piper 1997). Subordinate individuals would wait for opportunities to access resources rather than engaging in costly fights with more competitive individuals (Rohwer 1975, Ficken et al. 1990). Birds can learn to evaluate their chances in conflicts (Favati et al. 2017), but they can also interpret signals reflecting the competitiveness of others (Liker & Barta 2001). There are bird species that signal their social status and their corresponding strategies with colours and shapes of plumage characteristics (Liker & Barta 2001, Tibbetts & Safran 2009) or of bare parts, such as beaks or feet (Karubian et al. 2010, Velando et al. 2006). Variations in signalling traits may indicate alternative strategies (Chaine et al. 2018). However, if competition in groups becomes too high, even such strategies will hardly be successful and costs for subordinates will increase. Groups are likely to split because unequal competitors will separate spatially (could be similar to Marra 2000).

Here, we investigated how white-winged snowfinches, *Montifringilla nivalis* (hereafter snowfinches), cope with competition at feeding places in winter. The snowfinch is a typical species of high-elevation environments. The range of the European subspecies (*M.n.nivalis*) is restricted to alpine and nival zones of central and southern European mountains (Keller et al. 2020). Snowfinches use mountain habitats all year round (Heiniger 1991), even in winter when there is a permanent snow cover (Klein et al. 2016). There are only a few snow-free places, usually rocky ridges with strong winds or sun-exposed slopes, where birds can find food (Wehrle 1989). During this time of the year, snowfinches forage in flocks (Wehrle 1989), and consume seeds of various alpine plants, for example those of lady's mantle species *Alchemilla* spp., plume thistles *Cirsium* spp. (Wehrle 1989), eyebright species *Euphrasia* spp. and of sedges Cyperaceae (von Blotzheim 1988). Strinella et al. (2020) discussed that these natural food resources may become rarer with advancing climate change (Scheepens & Stöcklin 2013) and that this could increase competition within snowfinch groups. They suggested that females suffer more than males from climate change and concluded that there might be a sex-specific inequality in competitiveness. However, a basic understanding of social foraging in snowfinches is lacking to pursue such hypotheses. We think it is important to fill this knowledge gap, as climate change is progressing and snowfinches are potentially threatened by the consequences (Brambilla et al. 2016). To attract snowfinch groups for our study, we provided

supplemental food at anthropogenic feeding sites. We combined video recordings of foraging groups and observations of marked individuals to address the following three questions: (i) How is the competition situation in snowfinch groups at anthropogenic feeding sites? More specifically, we wanted to test whether snowfinch groups would split, if we offered them two food patches instead of one. We hypothesized that, under strong competition, some group members would prefer to feed at a free food patch rather than continue feeding with the group at another patch. Further, we aimed to show competition based on an increasing number of agonistic interactions between group members with increasing group size. (ii) How do individuals within groups behave when foraging, and do males and females behave differently? Here we looked for differences in access to food and in individual agonistic behaviour. We expected that if some individuals in snowfinch groups were more competitive than others, they would occupy the most profitable spots at feeding sites. Males or generally more aggressive individuals might be the more competitive ones. (iii) Could the beak colour of snowfinches be a signal of competitive ability? Snowfinches have bright orange beaks in winter, which turn black in the breeding season. Bare parts are considered to be suitable signals of social status because, unlike plumage ornaments, they are less dependent on the time of moult (Karubian et al. 2010). Therefore, we thought beak colour could be a possible signaling trait in snowfinches.

2. Material and Methods

2.1 Study sites and food patch set up

We observed snowfinches during the winter 2020/21, in 28 days between December and April, at artificial feeders in three winter sport centres located in the Swiss Alps, namely St. Moritz (46°30 N, 9°49 E, 2490 m asl), Melchsee-Frutt (46°46 N, 8°16 E, 1900 m asl) and Tiefenbach (46°35 N, 8°27 E, 2100 m asl). Snowfinches regularly come to these touristic areas to use anthropogenic food sources as long as there is a closed snow cover. Therefore, visits were carried out in harsh weather conditions, on days with snowfall, low temperatures, and a thick snow cover. We selected the areas because residents, who have been feeding the birds for several winters, allowed us to enter their properties

and to use their feeding sites. Natural, snow-free foraging sites of snowfinches are constantly shifting depending on wind and precipitation and are difficult to reach. The feeding site in St. Moritz and the one on Melchsee-Frutt, however, are well accessible with cable cars and ski lifts and are situated close to ski slopes. Tiefenbach is a halting place for touring skiers and snowshoe hikers, where the birds are fed in front of a hotel.

We offered the snowfinches two food patches in the immediate vicinity of their usual feeding sites (up to 30 m away). In the middle of each food patch was a bowl, 30 cm in diameter and 4 cm deep, filled with unpeeled sunflower and hemp seeds. The bowl was embedded in snow to avoid hostile reactions of snowfinches to this object foreign to them (Fig.1). Around the bowl, we marked out circular zones with wooden sticks, where food spillage occurred. We defined a first zone, 15 cm away from the edge of the bowl, a second zone another 20 cm and a third one another 25 cm away (Fig.1). The three zones allowed us to describe the uneven distribution of the spill, as the first zone contains the largest amount of seeds, the third zone the smallest. This is particularly important when measuring access to food of individual snowfinches. So, every food patch contained one bowl (also called zone 0) and three zones around it. Everything outside the food patch, where there were no seeds, was called zone 4. At the beginning of data recording, we placed the two food patches in preferably undisturbed positions (not standardised, but the same on every field day), with the bowls separated by 6-8 m, a distance that allowed groups of snowfinches to forage independently. The patches were always placed so that the birds and the observer could see both patches simultaneously.

2.2 Video recording of competition in snowfinch groups

We video recorded the two food patches in 34-minute sessions (+5min) with two camcorders (Panasonic HC-V180), mounted on a tripod, and placed 3-4 m away from the food bowls. We did 2-4 video sessions per field day, separated by at least one hour, which allowed us to sample throughout the day without depleting the camcorders' battery power or storage capacity (256 GB SD card). To ensure that there was always enough food for the birds, we filled up the food bowls before each

session. The proportion of seeds eaten after 34 minutes was often very small compared to the total amount.

We measured ambient temperature (with locally installed measuring devices) and wind strength (Beaufort scale) for every session and noted whether there was precipitation or not.

The video editing was done with DaVinci Resolve version 17.2.1. For all sessions, we had to combine the recordings from two camcorders, because one camcorder filmed one food patch each (Fig.1). To do so, we looked for a unique sound that occurred in both recordings and used it as a reference point to link them. After, we produced split-screen videos that showed both recordings simultaneously side by side (Appendix A). We ended up with 64 split-screen videos; however, 14 sessions had not been edited, because no snowfinches came to the feeding sites, fog impaired the view, or a camcorder failed.

Using video playbacks, we counted the number of birds at each food patch (including zone 0-3) every 20-s (referred to as counting points). During intervals from 10 s before to 10 s after these counting points, we estimated the number of agonistic behaviours within the snowfinch group, feeding at the patches (By group we refer to all the birds present at the feeding site). As agonistic behaviours, we included fighting, threatening (arched back), chasing, pecking, and jumping at each other (Ethogram in Appendix B). Video sequences with large groups of birds were slowed down to avoid missing any agonistic interactions. As well, to counteract counting errors, we listened for threatening sounds of snowfinches (von Blotzheim & Bauer 1997) and counted these as agonistic behaviours, when we could not visually detect them (in about 20% of the agonistic behaviours we observed, we could hear threatening sounds). If the behaviour of the snowfinches was clearly influenced by external disturbances, such as people passing by or foraging alpine choughs, we excluded the affected video sequences from analysis.

For statistical analysis, we used two different models; a binomial model with logit function to estimate the probability of various sized snowfinch groups to split between two food patches and a zero-inflated model to estimate the correlation between the number of agonistic behaviours and group size.

In the binomial model, we only considered 20-s counting points where we counted more than one individual (A group consists of at least two individuals) and this was the case at 3036 points. However, every third of these points had to be sorted out to avoid temporal correlation. We then modelled snowfinch groups, present at these points, as either split, if both food patches were occupied, or as together, if only one of the two patches was used. We included group size (total number of birds at the feeding site) and precipitation (yes, no) as predictor variables. Precipitation could restrict birds' vision so that they do not perceive both food patches, which would reduce the probability of group splitting. Group size was centred and scaled (mean set to 0 and standard deviation to 1) prior to the analysis. We used field day within feeding site as a nested random factor to account for differences in behaviour depending on time and location (more details in table 1, section a). A spatial preference for one of the food patches could have led to an incorrect estimation of the probability of group splitting. Therefore, we calculated daily preference values for both food patches (patch position varied between days, not within) based on how often snowfinch groups used them (Appendix C). We excluded field days from analysis where groups used one food patch more than 3 times as frequent as the other, so days when one of the patches was clearly preferred.

For the zero-inflated model, we calculated the average number of agonistic behaviours per individual in a group (total behaviours/group size) for every 20-s video interval and used it as response variable (square root transformed). Again, intervals in which no or only one individual was counted were excluded. Predictors were group size (log-transformed), temperature, wind, and precipitation (all weather variables were centred and scaled). The use of multiple weather variables is due to the assumption that agonistic interactions are very energetically costly and therefore tend to occur in more favourable weather conditions. We used day as a random factor. The zero-inflated model consisted of a Poisson model with log-link function and a binomial-model with logit-link function. We assumed a constant proportion of zero values ($z_i=1$). The model is shown in table 1, section b.

2.3 Observations of colour-ringed individuals

We surveyed individual access to food and aggressive behaviour by observing and following colour-ringed snowfinches. The ringing started six years ago and is part of a research and monitoring

project of the Swiss ornithological institute in Sempach, investigating snowfinch population dynamics. Birds were trapped by mist nets or nest traps at multiple feeding sites distributed throughout the Swiss Alps, including the study sites visited here (during the data collection for this study, there was no trapping). Each bird was marked with a metal ring and a light grey plastic ring with an alphanumeric code. We also collected saliva samples for DNA extraction used for sexing (Methods not published). Sexing based on DNA is probably the most reliable method because plumage characteristics cannot always be linked to one sex only (Strinella 2013).

In 2-3 one-hour sessions per day, which always alternated with video recordings, we waited for approaching snowfinches, about 15-25 m away from the food patches. As soon as the birds started feeding, we used a scope (Swarovski ATX or BTX) to look for a ringed individual and to follow its movements for up to three minutes. The exact observation time per individual depended on how soon the snowfinches left the food patch; we had an average observation time of 90 s (SD ± 67 s). Observations sometimes had to be interrupted because alpine choughs were displacing snowfinches from the feeding site. In addition to the ring number of the individual, we constantly recorded its position on the food patch, using the previously defined zones 0-4 (see Fig.1), and the time spent at the respective position. Position data should provide information on how close a bird can get to the most profitable zones, which allows an estimate on individual access to food. Further, we focused on agonistic interactions in which the focal individual was either actively involved (attacking) or passively involved (being attacked). Number of competitors was recorded at the beginning of each observation and only at the food patch used by the focal individual. Data recording parallel to observation could be managed with a voice recorder (Audio Memos App for iPhone) that automatically saves the recording time and duration. In a day, we managed an average of 11 (SD ± 7) observations of ringed individuals. We tried to select the individuals as randomly as possible, which means independent of their starting position. To always guarantee enough food, we filled up the food patches with seeds before each session.

We started analysis by calculating a weighted mean position for each observation, a number between 0 and 4, depending on the zones visited by the focal individual and weighted by the time it

spent in each zone. For individuals that were observed more than once, we determined the mean of all weighted mean positions and called this the individual mean. Individual variance between observations was indicated with relative distances between the weighted mean position for each observation and the individual mean. We used a Poisson model with log function to estimate a relationship between involvement in agonistic interactions (total number of interactions in which an individual was either passively or actively involved) and the access to food (weighted mean position) at two levels: firstly, between all observed individuals and, secondly, within individuals that we observed several times. While former is to give an overall impression, the investigation on the individual level is to identify possible differences between individuals regarding their agonistic behaviour and their position at the food patch. To examine both levels, we used individual mean and relative distance as predictor variables in the model. Other predictors were number of competitors, temperature, wind, and precipitation (we took the mean weather data from all video sessions that took place on the same day as the focal observations). We centred and scaled the number of competitors and the weather variables. As random factors, ring number and day were used (model in table 1, section c).

2.4 Measuring beak colour

We categorised and identified beak colour patterns using re-sighting photos of ringed snowfinches (not standardised) collected in winter 2020/21. Snowfinches change their beak colour from yellow to black between December and April to June (von Blotzheim & Bauer 1997), which regularly leads to different beak patterns with various amounts of black and yellow. We designed 10 categories of patterns that gradually reflect the progression of the beak colour change (Fig. 2). Category 1 corresponds to a yellow beak and category 10 to a completely black beak. For each re-sighting photo, an observer (A.C.G) noted the date the photo was taken, the ring number of the snowfinch and assigned the bird a beak colour score between 1-10, according to the categories. In the case of birds with beak patterns representing a transitional form between two categories, half-scores were used. We analysed only one photo of each individual per field day, as we assumed that beak category does not change within a day.

To find out if beak colour is related to the aggressiveness of snowfinches, we linked beak scores to information about agonistic interactions, collected in the focal observations. More specifically, we assigned a beak score to each focal observations if both measurements were collected on the same day. The proportion of agonistic interactions in which an individual was active (attacking) is an estimate of aggressiveness and was therefore used as the response variable here. We had two levels, active or passive involvement in an agonistic interaction, so we worked with a binomial model with logit function. Beak score and day of year were predictor variables. The latter was needed to take the seasonal colour change of the beak into account, as we were more interested in the individual differences in beak score. Ring number and sampling day were used as random factors (table 1, section d).

2.5 Statistics in general

All statistical models used, are described in chapters 2.2-2.4, here follows information on the general procedure of the statistical analysis. We used R version 4.0.2 (R Development Core Team 2021) to analyse our data. We fitted most of the models with the function `glmer`, package `lme4`. The exception was the zero-inflated Poisson model, which we fitted with the function `brm`, package `brms` (Bürkner 2017), using uninformative priors. We assessed fit of all models by visual residual analyses. Models were checked for overdispersion by comparing residual deviance with residual degrees of freedom or by using the function `dispersion_glmer` (package `blmeco`). For all models, we used 2000 simulated random values from the joint posterior distribution of model parameters to describe parameter estimates and their uncertainty. We used the median as point estimate and specified 2.5% and 97.5% quantiles as lower and upper limits of the 95% compatibility intervals.

3. Results

3.1 Competition in snowfinch groups

On 14 of 28 field days, snowfinches had no clear preference when choosing one of the two food patches we offered. On these days we recorded 35 videos and counted the number of birds at 486

time points in the video (in 1 min intervals). We observed groups of 2 up to 72 individuals. On average one group included 12 (SD \pm 13) individuals. At 235 counting points, all snowfinches stayed together at one food patch, at the other 186 points, groups split between the two patches. The between location standard deviation was close to zero and the between-field day standard deviation was 1.02. Based on the logistic regression, group splitting probability was positively correlated with group size (Fig.3, black line). However, a positive correlation was to be expected, because if the birds had decided completely independently of their conspecifics which food patch to choose, splitting probability would be $1-0.5^{(n-1)}$, with n being the number of individuals present. We illustrated in Fig. 3 with a purple line, how this hypothetical splitting probability would change with group size. Compared to the purple line, we found a much slower increase in splitting probability with increasing group size. Splitting probability in a group of 15 individuals is expected to be almost 100% assuming an independent distribution of the snowfinches to both food patches, whereas we observed a probability of 61% (CrI: 47-73%). Moreover, splitting probability was smaller with precipitation (39% CrI: 20%-62%) than without (62% CrI: 48%-75%).

In the 64 split-screen videos, we counted the total number of agonistic behaviours in snowfinch groups during 3398 20-s intervals. We observed an average of 0.3 agonistic behaviours (SD \pm 0.9) per interval. In 2843 intervals there were no agonistic behaviours at all. Group sizes ranged from 2 to 65 individuals with an average of 12 individuals (SD \pm 11). The between-field day standard deviation was 0.52. Our zero-inflated model showed an increasing proportion of zero values (intervals with no agonistic behaviour) with increasing group size, meaning that the model estimates a decreasing probability of agonistic behaviour with increasing group size. The mean number of agonistic behaviours per individual clearly seemed to decrease the larger groups were (Fig.4). The more wind and the higher the temperature, the more likely were agonistic behaviours. With precipitation, it was less likely that agonistic behaviours will occur than without. All model estimates can be seen in table 2, section b.

3.2 Individual social behaviour and access to food

Between January and April 2021, we made 239 observations of 108 ringed individuals. 53 individuals could be observed only once, the other 55 between 2 and 10 times, resulting in an average of 2.4 observations per individual (SD ± 1.9). Of all the individuals, 43 were female and 191 males. We had repeated observations of 9 females and 40 males. The observed snowfinches were seen in groups of 14 individuals on average (SD ± 12). In 65 of all observations, focal individuals were involved in 1-8 interactions. In the remaining 194 observations we saw no interactions at all (mean of 0.5 interactions per observation, SD ± 1.1). Individual mean position at a food patch was on average 1.8, SD ± 1.0 (possible numbers were 0-4).

Using the Poisson model, we found a negative correlation between the number of agonistic interactions, in which focal individuals were involved, and the individual mean position in which they foraged (Fig.5a, estimated slope -0.23, CrI: -0.55 to +0.09). If individual mean positions were increased by 1 (one zone further away from the bowl), the involvement in interactions would decrease to 79% (CrI: decrease to 58% - increase by 9%).

Within individuals we measured several times, our model also suggested a slightly negative correlation between the number of agonistic interactions and the position at the food patch (here given by the relative distances). This implies that individuals are less likely to be involved in interactions when feeding in zones further away from the food bowl than in zones close to it. The slope most compatible with our data is -0.07 (CrI +0.30 to -0.17). Figure 5b shows the individual regression lines.

Compared to the slope of the regression line in Figure 5a, the slopes of the individual regression lines (Fig. 5b) are smaller. This difference occurs because there are variations in involvement in agonistic interactions and position at the food patch between individuals and not only within individuals. We observed individuals across different ranges of positions on the food patch (See the beginning and the end of the regression lines in Fig. 5b). For example, some individuals moved only between zones 0 and 1 and others only between zones 3 and 4. Further, individuals differed in the number of agonistic interactions they have been involved in (random intercepts between -0.53 and

1.55). Individuals that moved only in zones close to the food bowl tended to be the ones involved in more interactions.

In Fig. 5b, the regression lines are coloured according to sex. Among the individuals, often involved in agonistic interactions (high intercepts), there seemed to be no females. However, in total, we observed considerably fewer females than males. Moreover, individuals were clearly involved in fewer interactions as group size increased. Weather variables did not seem to have large effects on the number of interactions (model estimates in table 2, section c). The between-day SD was 1.0 and the between-ring SD was 0.7.

3.3 Beak colour

We assigned a beak colour score to 153 beaks belonging to 105 different individuals. We identified 25 of these individuals as females and 110 as males, 18 remained unknown. Individuals could be photographed between 1 and 6 times during the winter season (Mean: 1.4, SD ± 0.9). The first photos were from early December 2020, the last ones were taken in mid-April 2021. With the assigned scores, we were able to illustrate the seasonal beak colour change of snowfinches (Fig. 6a). At the beginning of the season, in December, we had beak scores from 1 to 3.5 and at the end, in April, scores from 8 to 10. The first bird with a completely black beak was observed in early March. We also compared seasonal beak colour change of those 12 individuals, from which we had 3 or more photos (Fig. 6b). The beak colour change of some individuals seemed to start earlier in the season than in others. The rate at which the beak colour of snowfinches changed, differed only slightly between individuals.

Beak scores varied not only within the season, but also within days (mean scores with SD are given in table 3). Especially in March, daily variances in beak scores were large (Fig. 6a). Individuals could differ by up to 5 score points on the same day. Sex does not seem to fully explain these individual differences because beak scores of the 25 females were not remarkably higher or lower than those of males (Fig. 6a).

We were able to assign a beak score to 41 individuals in 76 focal observations. The assigned beak scores ranged from 2 to 10 (mean score 7, SD ± 2.6). Observations were done on 17 field days from

beginning of February until mid-April. During an observation, individuals were involved in an average of 0.7 (SD \pm 1.4) interactions and were active in 0.2 (SD \pm 0.6) interactions and passive in 0.5 (SD \pm 1.2). However, in 51 observations, focal individuals were not involved in any interactions. Our model suggested a positive correlation between the proportion of interactions, in which an individual was active, and its beak colour score (Fig. 7). Snowfinches with black beaks were therefore the ones that were active in the highest proportion of interactions. But, a slightly negative slope would also be possible, as our data is most compatible with slopes between -0.6 and +3.5 (95% CrI). All model estimates are listed in table 2, section d. The between-day SD was 0.32 and the between-ring SD was 1.4.

4. Discussion

4.1 Competition in snowfinch groups

We offered the snowfinches two equivalent food patches to choose from. In our case, choosing means that they could either use the food patch where conspecifics were already feeding, or the free food patch without conspecifics. We investigated the probability that a group of snowfinches would split between the two patches, respectively the probability that at least one of the birds would choose the free patch. We found an increase in splitting probability with group size. However, the increase was slower than we would have expected for a hypothetical group, in which each bird chooses a patch independently of the others. Accordingly, snowfinches preferred to go to the food patch that has already been occupied by conspecifics, rather than feeding on the free patch. They seemed to stay in their groups and to avoid splitting up between both patches. This then changed in groups of more than 60 individuals. Members of such large groups almost always used both food patches. Moreover, we observed a generally smaller probability of group splitting with precipitation than without.

An additional food patch should increase the proportion of birds that have access to food (Delestrade 1999). Especially for less competitive individuals, using the additional food patch would be a

possibility to avoid competing with group members. The reason why snowfinches in groups of less than 60 individuals rarely used the free food patch, seems to be, that advantages of staying in groups outweigh the reduced access to food (Delestrade 1999) and the increased competition (Krause & Ruxton 2002, Rose & Soole 2020) at the patch with conspecifics. One of these advantages could be a generally reduced predation risk (Dehn 1990) due to increased vigilance in groups (Benkman 1997, Boland 2003), faster predator detection (Boland 2003) or dilution effects (Bertram 1987). Individuals who stay in the middle of the group or very close to their conspecifics benefit most from group protection, while those on the edge, foraging further away, are often the first to be caught in a predator attack (Krause & Ruxton 2002, Hirsch 2007). Snowfinches that separate from the group to feed on the free food patch may therefore be more vulnerable to predators, why they prefer to choose the occupied food patch. This hypothesis would also be in line with our result that snowfinch groups are less likely to split during precipitation because poor visibility during precipitation could prevent birds from quickly detecting predators, why they may rely even more on group protection. Potential predators of snowfinches include stoats *Mustela erminea*, birds of prey such as sparrowhawks *Accipiter nisus*, and domestic cats *Felis catus* (unpublished observations of these species lurking in foraging areas of snowfinches). In addition to predator pressure, snowfinches may prefer to stay in groups because this helps them to cope better with unfamiliar conditions (Liker & Bókony 2009). Both the many ski tourists at our study sites and the unusual food patch setup, with bowls and sticks, were potential stressors that the birds don't face at their natural feeding sites. Being in a group could lower the fear of new, unknown objects or situations (Day et al. 2001, Dardenne et al. 2013). More bold and explorative individuals might encourage neophobic individuals to follow them (Stöwe et al. 2006), why all individuals would end up flying to the same food patch.

Snowfinch groups of more than 60 individuals almost always split between both food patches. This group size is potentially the limit, where competition cancels out group advantages such as reduced predation risk or social facilitation. At only one food patch, room becomes too tight for all individuals, and they cannot all get to the food. Under these circumstances, it might be more profitable to take higher risks and visit the second food patch.

We further wanted to explore competition in snowfinch groups based on the number of agonistic interactions between group members. In contrast to many studies that found an increase in agonistic interactions with group size (Benkman 1997, Johnson et al. 2004, Rose & Soole 2020), we found a negative correlation between mean number of agonistic behaviours per group member and group size. According to the hypothesis of Estevez et al. (1997), birds (here domestic fowls) can adapt a low-aggressive, tolerant strategy in large groups. Domestic fowls establish dominance hierarchies to avoid repeated excessive and energy-consuming contests (Smith 1974). When domestic fowls are kept in large groups, the probability of group members meeting multiple times decreases. Establishing a hierarchy would then be costly, why they instead adapted a tolerance strategy (Estevez et al. 1997 & 2003). Although we do not know how stable winter foraging groups of snowfinches are and whether snowfinches form social bonds, we think that the tolerance strategy could explain our results. Social structures in winter flocks were found in several bird species (for example Aplin et al. 2013, Block 2021). In small groups, snowfinches may know each other and use agonistic interactions to determine their ranks. On days, when natural food is hard to find, many individuals from different groups, whose social bonds are weak, might gather at artificial feeding sites. Under these conditions, a hierarchy would only have a short-term benefit, because large groups will separate again (del Mar Delgado et al. 2021).

Another explanation for the negative correlation of agonistic behaviours with group size, could be that individuals face a trade-off between defending a food patch and acquiring as much food as possible per time unit (similar to Schoener's model of optimal territory size 1983). Individuals in small groups might benefit from preventing others from feeding in the relatively compact patch, because during phases of victory, they can quickly gain a lot of food for themselves. But if the number of competitors increases, the effort to defend a patch becomes greater and the time to consume food decreases. Individuals in large groups would therefore give up displaying agonistic behaviours once the defence effort exceeds benefits in foraging. However, what remains questionable about this hypothesis is whether snowfinches can obtain any advantage at all by defending a food patch. In this study, the food was never limited, and it consisted of distinct, small seeds that would have been shareable between group members. As long as there was enough room

at the food patch, several snowfinches could probably have eaten their optimal amount of food without inducing agonistic interactions.

Competition in snowfinch groups is likely to increase with group size, despite rare agonistic behaviours. Individuals may use signals, such as beak colour or feather ornaments, to indicate their social status rather than fighting with each competitor (Pagel & Dawkins 1997). Individuals may also become more stressed as group size increases because the patch gets crowded. Under stress, snowfinches might rather concentrate on getting enough food instead of fighting.

We observed that the probability of agonistic interactions in snowfinch groups decreased with precipitation and increased with rising temperatures. With precipitation, food at natural feeding sites becomes scarcer as many resources are covered under snow. Snowfinches at our artificial feeders might therefore concentrate more on getting enough food than on social interactions. At high temperatures, when the snow melts, the opposite would be the case. Furthermore, when visibility is reduced due to bad weather, birds must be more vigilant because of predators and agonistic interactions would then be too risky.

Taken together, we found no evidence of strong competition in the snowfinch groups. Instead, they seem to benefit from being in a group, which could be related to better protection against predators or social facilitation when foraging. These groups advantages become stronger in phases of precipitation and cold temperatures. With increasing group size, competition seems to increase slightly. Displaying of agonistic behaviours is not directly related to increasing competition but could serve to establish or strengthen social bonds.

4.2 Individual social behaviour and access to food

We found that foraging snowfinches were slightly more involved in agonistic interactions in the centre of a food patch than in the periphery. This is partly explained by the fact that individuals moving towards the centre, became more involved in interactions. However, we also found differences between individuals in their agonistic behaviour and their position at the food patch.

There were individuals that mainly fed in the centre and hardly used outer zones around the food bowl. These were also the ones who were involved in more interactions than their conspecifics.

We set up our food patches in a way that the amount of seeds was largest in the centre of the patch and decreased towards the outside. Snowfinches that fed in the centre, probably had better access to food and higher feeding rates than their conspecifics (Johnson et al. 2004). Individual differences in access to food are often discussed in birds living in socially structured groups (Carrascal et al. 1988, Ficken et al. 1990, Stahl et al. 2000). Subordinates know their status and try to avoid conflicts by allowing dominant individuals to use the best feeding sites. For example, in flocks of black-capped chickadees, dominant birds visited feeders at any time, even when occupied by conspecifics, while subordinates were more likely to wait until feeding sites became free (Ficken et al. 1990). In a similar way, subordinate snowfinches may have avoided feeding in the middle of the food patch to prevent conflicts with dominants and waited in outer zones for a chance to get food. Dominant snowfinches, on the other hand, could use central positions at any time. However, these hypotheses presuppose that snowfinches in a group know each other and establish hierarchies. In male domestic fowls, aggressiveness was the best predictor of an individual's social rank (Favati et al. 2017). The more aggressive an individual was, the more likely it became dominant. If we assume, that the snowfinches feeding in the centre of the patch were the dominants, these would have also been those involved in most agonistic interactions. Rank could depend on aggressiveness in snowfinches.

According to our model, also a slightly positive correlation between involvement in agonistic interactions and position at the food patch would have been compatible with our data. Individuals in the outer zones of the food patch may be involved in as many (or more) interactions as individuals in the centre. Conflicts in outer zones could result from limited accessibility to seeds.

Among the individuals most involved in interactions, we only found males. It could be concluded that females are subordinate to males. This has been shown several times in bird groups in winter (Carrascal et al. 1988, Kubitza et al. 2015, Krams et al. 2020). However, males and females of snowfinches seem to differ little in access to food. We think that dominance of females does not necessarily need to be linked to aggressiveness, but that other factors such as body size, age or

personality traits can be important (Dingemanse & de Goede 2004, Hermann 2017). In addition, we observed considerably more males than females at the food patches. It is possible that we did not observe the aggressive females, either by chance or because they were not ringed. There is not necessarily a difference in aggressiveness between the sexes. The absence of females in snowfinch groups could, however, indicate that they are not strong enough to compete with males (Marra 2000). The females may have separated from males and migrated to other regions (Resano-Mayor et al. 2020).

4.3 Beak colour

We described how snowfinches changed their beak colour from yellow to black in the winter season (or nonbreeding season in case of the snowfinch). During this process, different beak patterns of yellow and black areas emerged, with the black areas becoming larger towards the breeding season. All snowfinches seem to change their beak colour, but we found individual differences in the temporal occurrence of beak patterns. Our observations suggest that these differences are due to some individuals starting the colour change earlier than others or progressing the change faster. We can say that beak colour is probably not a sex-specific trait, there are females as well as males that already had black beaks early in the season. However, Individual differences in the expression of a trait lay the basis for a trait to serve as a signal. Our model estimated that individuals with a larger amount of black in their beaks initiated more agonistic interactions than those with a more yellow beak. Despite the high degree of uncertainty, shown by the extended credible interval, we consider the possibility that snowfinches signal their competitive ability with an early and rapid colour change to black.

The black colour of feathers and bare parts of birds is usually determined by the pigment melanin (McGraw 2006). Several bird species are thought to use melanin colouration to signal their individual quality (Piault et al. 2012) and their aggressiveness in the context of breeding (Karubian et al. 2010, Thys et al. 2020) or in the context of competing for food (Senar & Camerino 1998, Liker & Barta 2001). Some studies have also specifically investigated the signalling effect of melanin-coloured beaks. For example, Laucht et al. (2010) showed that testosterone levels of male house sparrows

correlated with beak colour and concluded that a dark beak could be a signal for testosterone-related aggressiveness. House sparrows change their beak colour from a pale horn colour to black between the non-breeding season and the breeding season (Witschi and Woods 1936), which was reflected in the seasonal variation of birds' testosterone levels in the study. In addition to this seasonal trend, Laucht et al. (2010) also found a large variability in individual beak colours and testosterone levels. They hypothesised that house sparrows with high testosterone levels and darker beaks may show different behavioural strategies than their conspecifics because testosterone was shown to influence behaviour in other animals (Adkins-Regan 2005). However, to our knowledge, a study attempting to find a link between beak colour of house sparrows and behavioural strategies, or aggression has not yet been published. Signals for aggression in birds, but also in house sparrows (Hegner and Wingfield 1986), have often been associated with sociality during the non-breeding season (Tibbetts and Safran 2009, Santos et al. 2010). When foraging in groups, it could be advantageous for subordinates not to engage in fights over food resources with dominant, aggressive individuals (Rohwer, 1975, Tibbetts & Lindsay 2008).

We saw, that snowfinches prefer to stay in groups during the non-breeding season. A signal for aggression could possibly have evolved in their case as well. The seasonality and individuality of the beak colour change may suggest parallels between snowfinches and house sparrows. A hormonal change in snowfinches could also affect their beak colour and their aggressiveness. In this way, snowfinches could use beaks to assess whether their competitors are reacting aggressively to their presence. Males as well as females could use the signal when feeding together (Lyon & Montgomerie 2012), which would fit our findings that there were individuals of both sexes that tended to change beak colour earlier than others. Moreover, young snowfinches have completely yellow beaks after fledging, while adults have black beaks during this time of the year (von Blotzheim 1997). Through a signalling effect of their beak, they could protect themselves from direct aggression from adults. Juvenile plumage in other bird species can have similar effects and can protect against attacks by adults (Muehter et al. 1997, VanderWerf & Freed 2003).

Another study on the signalling effect of beaks was done by Karubian et al. (2010). They showed in an experiment that dominant, breeding red-backed fairy-wren males signal their status with a black beak to differentiate themselves from the non-breeding auxiliary males. In the case of snowfinches, it is still uncertain whether there are breeding and helping individuals during breeding season, but we should not reject the idea that beak colour can also be a signal of mating and breeding readiness. Perhaps the beak colour also says something about the quality of the individuals, how successfully they can raise young or acquire food. Further research would be needed to compare beak colour with breeding success.

Our data, given the model, would have been compatible with the fact that beak colour is independent of aggressiveness, suggesting that there was no signalling effect. Given that all snowfinches change their beak colour seasonally and there seem to be no exceptions, the beak colour might not be flexible enough to act as a signal. Rather, the change in colour could be a result of the seasonally changing conditions in the mountains. Snowfinches could also use different signals instead of the beak colour. Similar to some Old and New World sparrows (reviewed in Tibbetts & Safran 2009), snowfinches have a black throat badge, which they sometimes display in agonistic interactions (pers. observations).

5. Conclusion

Our study provided first insights into the social behaviour of snowfinches in winter. We found little evidence of strong competition within foraging groups. On the contrary, snowfinches are likely to benefit from social connections. Seasonal challenges, such as the limited accessibility of food resources and the vulnerability to predators, are probably easier to face in groups than alone. Different foraging strategies among individuals, such as displaying agonistic behaviour to defend optimal positions at the feeding site or waiting for an opportunity to grab resources at the periphery, indicate that there might be a social structure within snowfinch groups. Likewise, signalling of aggression through beak colour would show that snowfinches often interact with conspecifics. The social behaviour of snowfinches in winter seems to be pronounced. In a next step, we could

investigate how groups are organized. Do the same individuals always form groups together or are there individuals that constantly join new groups? Here we studied the behaviour of snowfinches at artificial feeding sites. It is unclear to what extent our results and assumptions can be transferred to natural situations of snowfinches, because in tourist winter resorts there are various disturbance factors, the birds might be stressed, and their behaviour might be influenced. However, supplemental food from humans seems to be an important food source for many snowfinches, why we think it makes sense to continue research with these birds at artificial feeding sites.

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Tables

Table 1: Overview of all models used in statistical analyses. GroupSize=Counted number of Individuals at the food patches, Location= Study site, Melchsee-Frutt/St. Moritz/Tiefenbach, Doy=Day of year, Precipitation= Precipitation yes/no (1/0), Temperature= Temperature during data recording in degrees Celsius, Wind= Strength of the wind according to beauford scale, Ind.mean= Mean weighted mean position per individual at the food patch (zone 1-4), Reldist= Deviation of Ind.mean from mean weighted position per observation.

	Dependent variable	Model
a	Group splitting probability	GroupSize +Precipitation +(1 Location/Doy)
b	Number of agonistic Interactions	log(GroupSize)+Temperature+Wind+Precipitation +(1 Doy)+offset(log(GroupSize), zi=~1)
c	Number of agonistic Interactions	Ind.mean+Reldist+GroupSize+Temperature+Wind+ Precipitation+(1 RingNr)+(1 Doy)
d	Proportion of agonistic Interactions initiated	BeakScore+Doy+(1 RingNr)+(1 Doy)

Table 2: Overview of estimated model coefficients. Labels a)-d) correspond to the models described in Table 1. Mean, 2.5% quantile and 97.5% quantile are based on 2000 samples drawn from the joint posterior distribution. ".z" indicates centred and scaled variables.

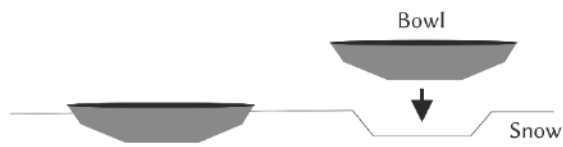
	Dependent variable	Independent variables	mean	2.5% quantile	97.5% quantile
a	Group splitting probability	Intercept	0.48	-0.08	1.06
		GroupSize.z	1.32	0.91	1.72
		Precipitation	-0.90	-1.89	0.04
b	Number of agonistic interactions	Intercept	0.44	0.12	0.75
		Zi_Intercept	0.91	0.77	1.06
		Log(GroupSize)	-1.28	-1.38	-1.17
		Temperature.z	-0.02	-0.25	0.22
		Wind.z	0.02	-0.21	0.25
		Precipitation.z	-0.17	-0.41	0.06
c	Number of agonistic interactions	Intercept	-1.03	-1.81	-0.29
		Ind.mean	-0.23	-0.54	0.08
		Reldist	-0.07	-0.29	0.15
		GroupSize.z	-0.51	-0.82	-0.20
		Temperature.z	0.01	-0.48	0.48
		Wind.z	-0.29	-0.97	0.38
		Precipitation.z	0.01	-0.52	0.52
d	Proportion of agonistic interactions initiated	Intercept	-1.49	-2.62	-0.38
		BeakScore	1.43	-0.58	3.57
		Doy	-1.01	-2.84	0.73

Table 3: Mean and SD of all beak colour scores (in total 153) recorded on every field day (in total 30 days).

Year	Month	Day of year	Beak score mean	SD	Sample size
2020	December	340	1.75	0.35	2
2020	December	342	2.56	0.81	9
2020	December	354	1.33	0.58	3
2021	January	21	2.00	NA	1
2021	February	32	3.00	1.00	3
2021	February	34	2.00	NA	1
2021	February	35	2.75	1.06	2
2021	February	37	2.58	0.79	12
2021	February	39	4.00	NA	1
2021	February	41	3.00	NA	1
2021	February	42	2.00	NA	1
2021	February	43	4.00	0.35	5
2021	February	49	4.20	0.84	5
2021	February	50	4.55	0.96	10
2021	February	51	5.33	1.03	6
2021	February	58	6.33	2.52	3
2021	March	60	5.83	0.29	3
2021	March	63	6.50	1.38	6
2021	March	64	7.33	1.51	6
2021	March	67	8.60	1.52	5
2021	March	70	8.00	1.00	3
2021	March	71	7.56	2.23	8
2021	March	72	9.00	1.41	2
2021	March	73	8.96	1.51	12
2021	March	77	9.50	0.84	6
2021	March	78	9.00	1.41	8
2021	March	80	9.64	0.75	7
2021	March	81	8.33	2.89	3
2021	April	96	9.77	0.44	13
2021	April	103	9.33	0.82	6

Figures

side view:



from top:

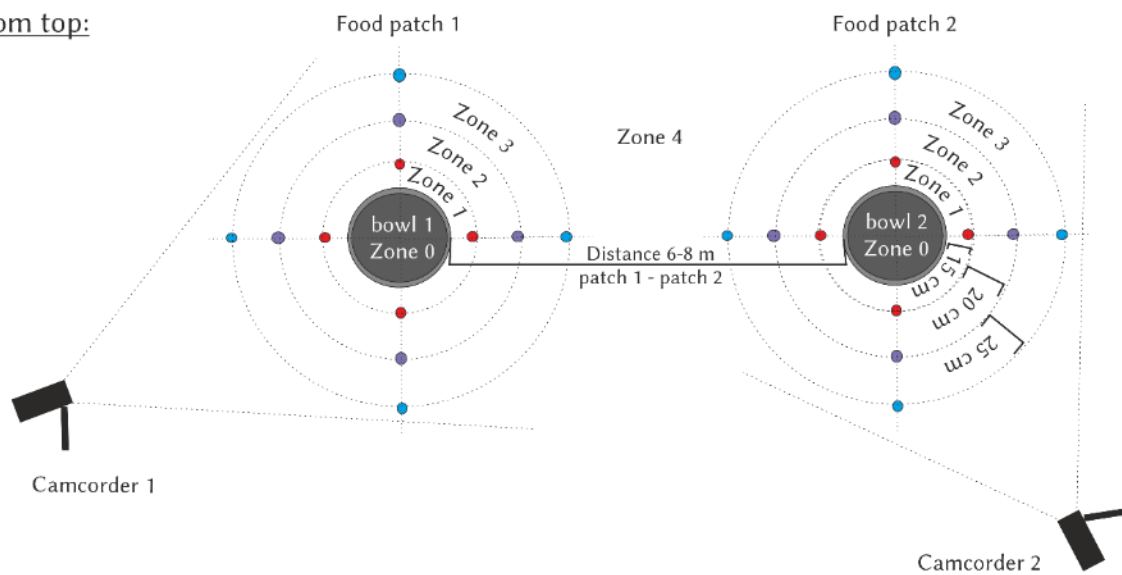


Figure 1: Set-up plan for fieldwork: Side view shows how the bowls were placed in the snow. Top view shows two complete food patches, each with a bowl in the middle and three zones, marked with wooden sticks (coloured points) around it. Dotted lines indicate which areas are marked by the sticks. Zone 4 refers to the whole area outside the patches. The areas recorded by the camcorders are indicated with dashed lines.

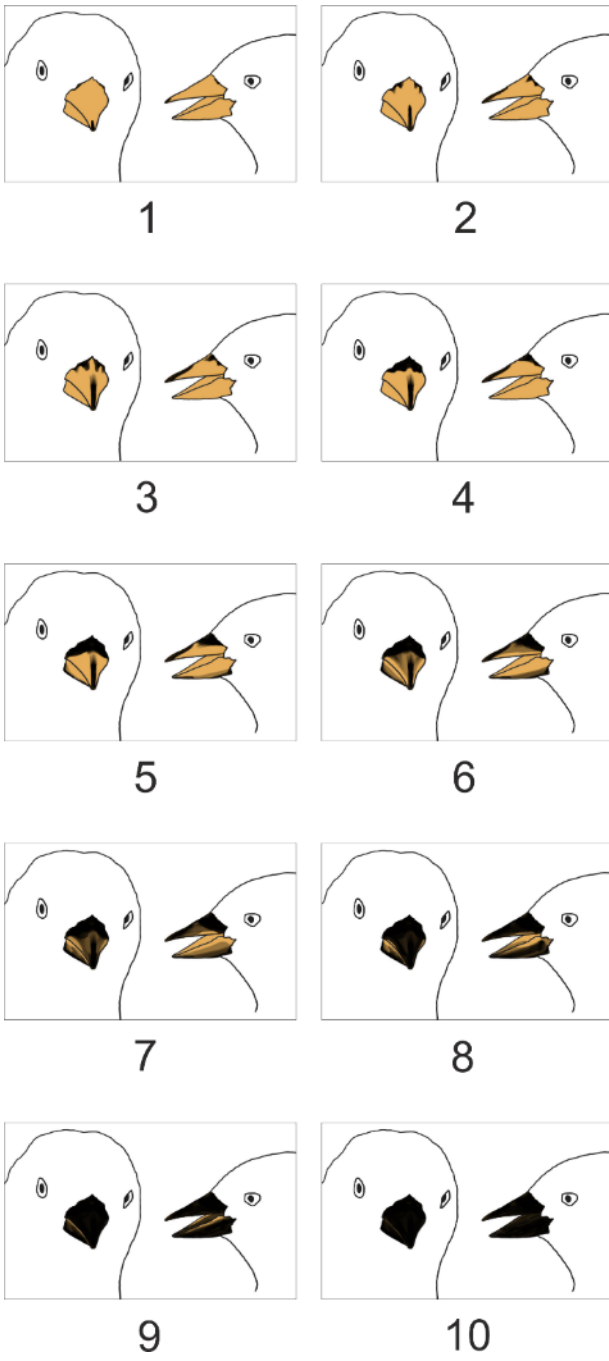


Figure 2: Beak colour pattern categories.
The numbers below each image correspond to the beak colour scores.

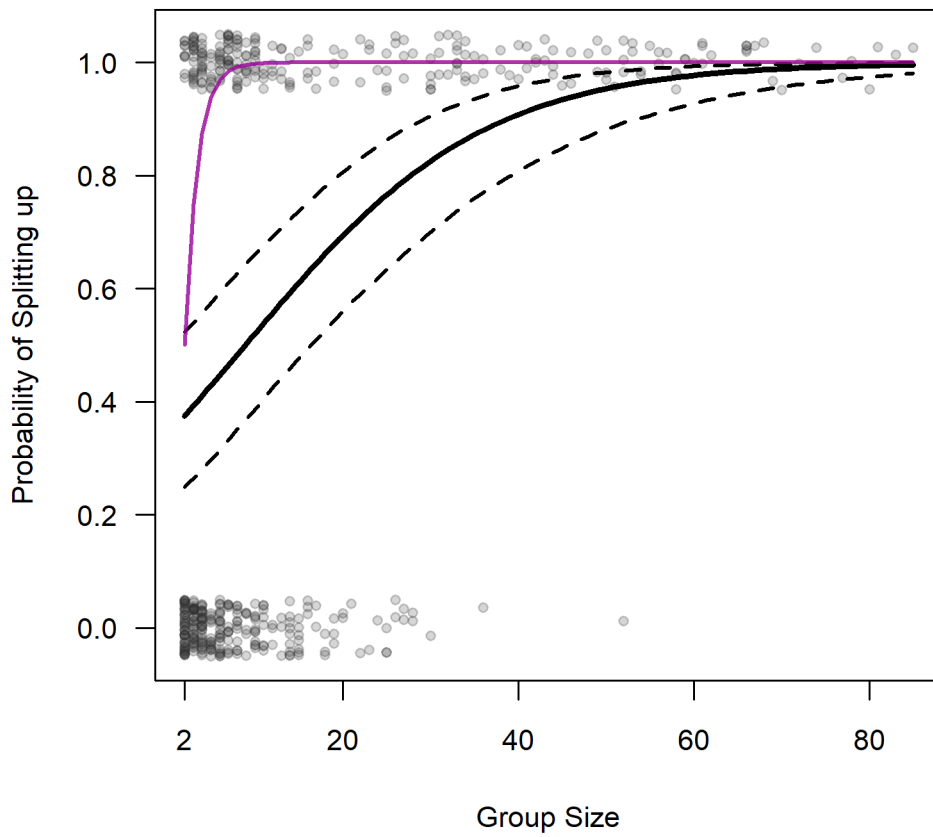


Figure 3: Probability that snowfinch groups split between two available food patches on days without precipitation. Estimates are based on a logistic regression. 95% credible interval is indicated with dashed lines. A splitting of 0.0 means that the groups stay together at one food patch ($n=235$), a splitting of 1.0 means that both food patches are occupied ($n=186$). Group size is the total number of individuals visiting the food patches at the same time. The purple line shows a hypothetical increase in splitting probability with group size, assuming that each individual in the group chooses a food patch independently of the others.

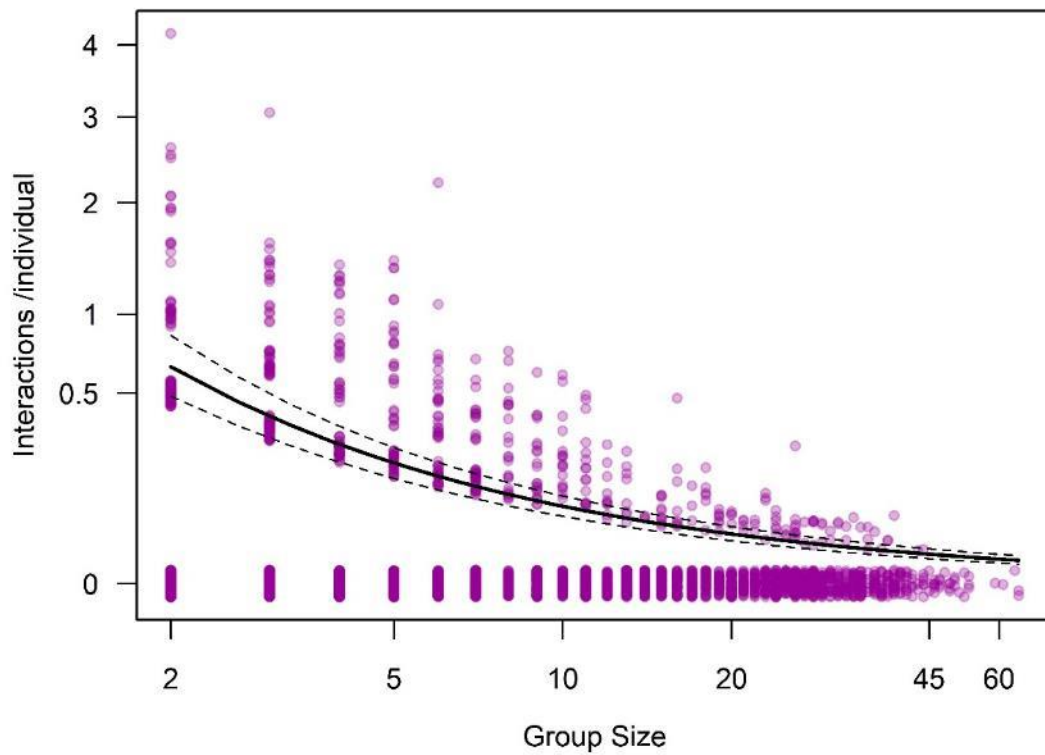


Figure 4: Correlation between group size (x-axis square root transformed) and mean number of agonistic interactions per group member and per 20 s interval (y-axis log transformed). Estimates based on a zero inflated model that assumes average weather conditions. 95% credible interval is indicated with dashed lines. n=3398

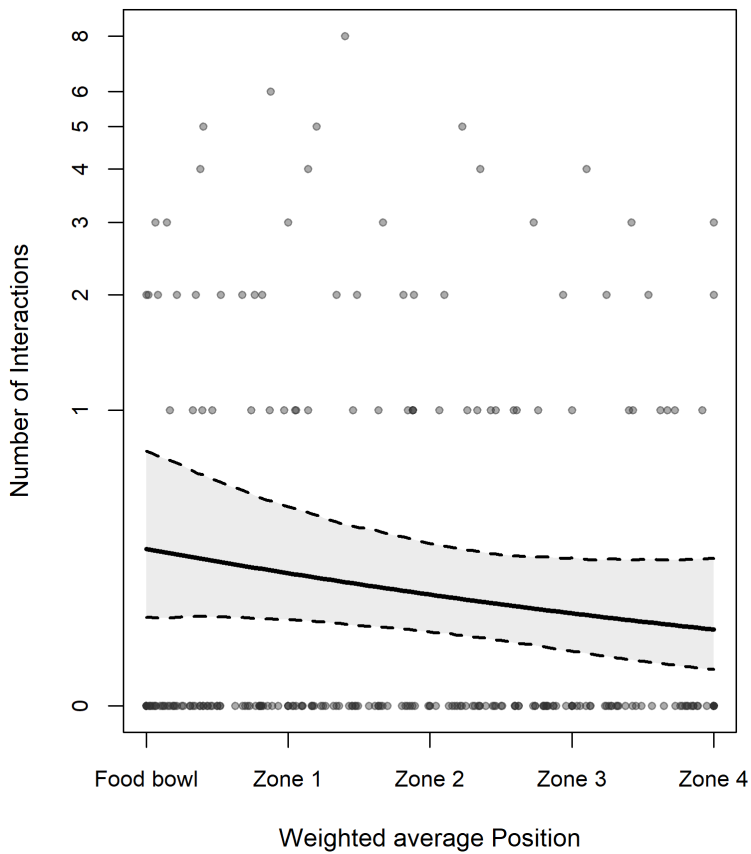


Figure 5a: Relationship between the number of interactions in which focal individuals were involved in (y-axis log transformed) and their mean position relative to the food patch, weighted by duration of stay (n=108). Food bowl is the middle of a food patch, zone 4 is furthest away (see Fig.1). Medium weather conditions are assumed. Regression line is based on Poisson Model and 95% Interval is indicated with dashed lines.

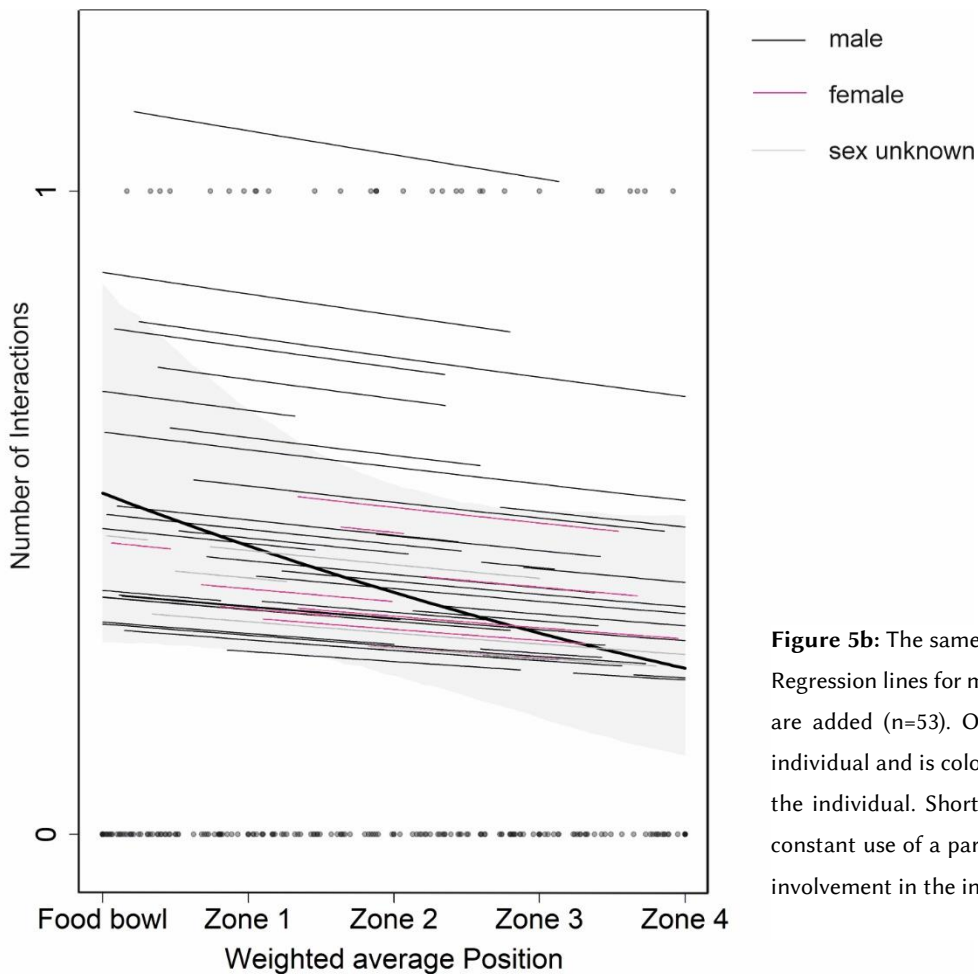


Figure 5b: The same plot as in a) but zoomed in. Regression lines for multiply observed individuals are added (n=53). One line corresponds to one individual and is coloured according to the sex of the individual. Short, horizontal lines indicate a constant use of a particular position with similar involvement in the interactions.

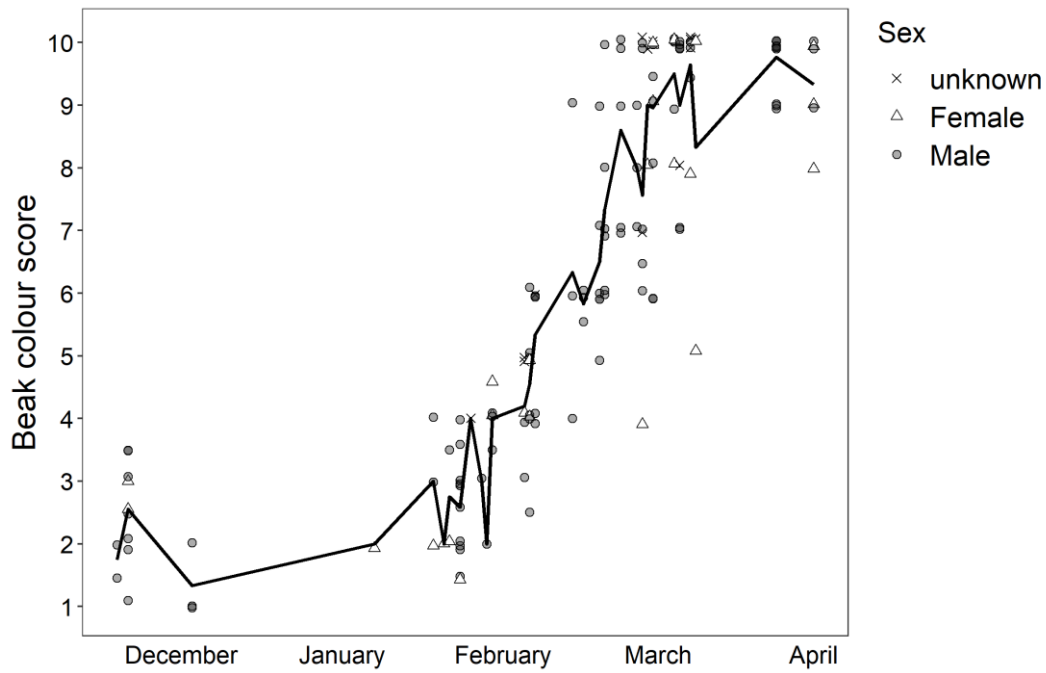


Figure 6a: Beak colour change of snowfinches over the course of the winter season 2020/21. Each point corresponds to the daily beak colour score of an individual. Score 1 corresponds to a yellow beak, 10 to black beak. The black line connects the daily mean scores. n=135

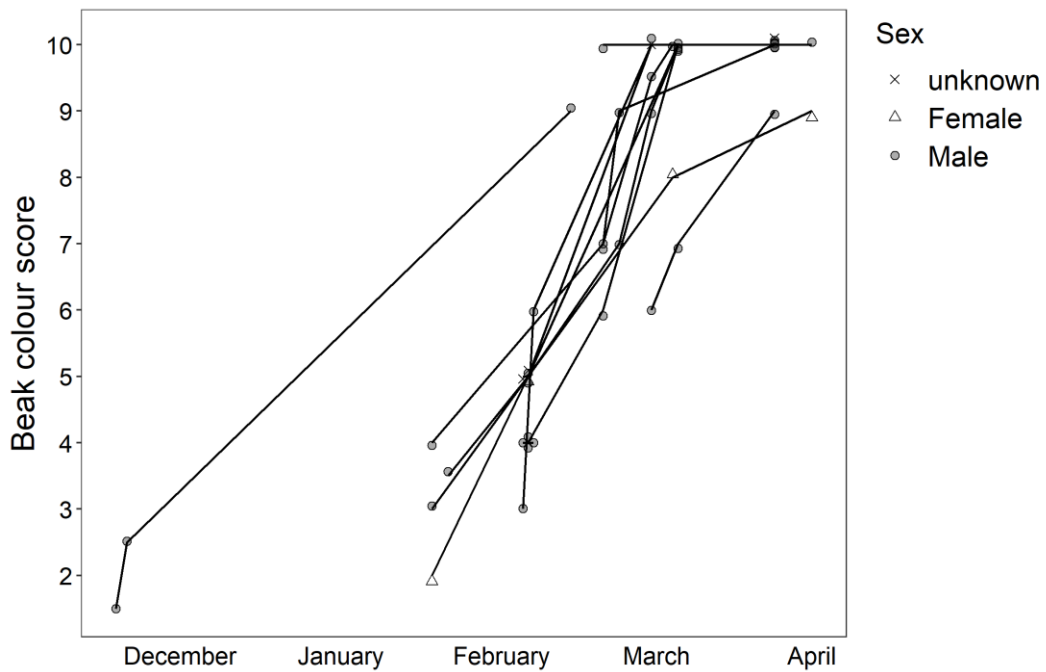


Figure 6b: Beak colour change in single individuals. Each line belongs to an individual whose beak colour was recorded at least 3 times. n=10

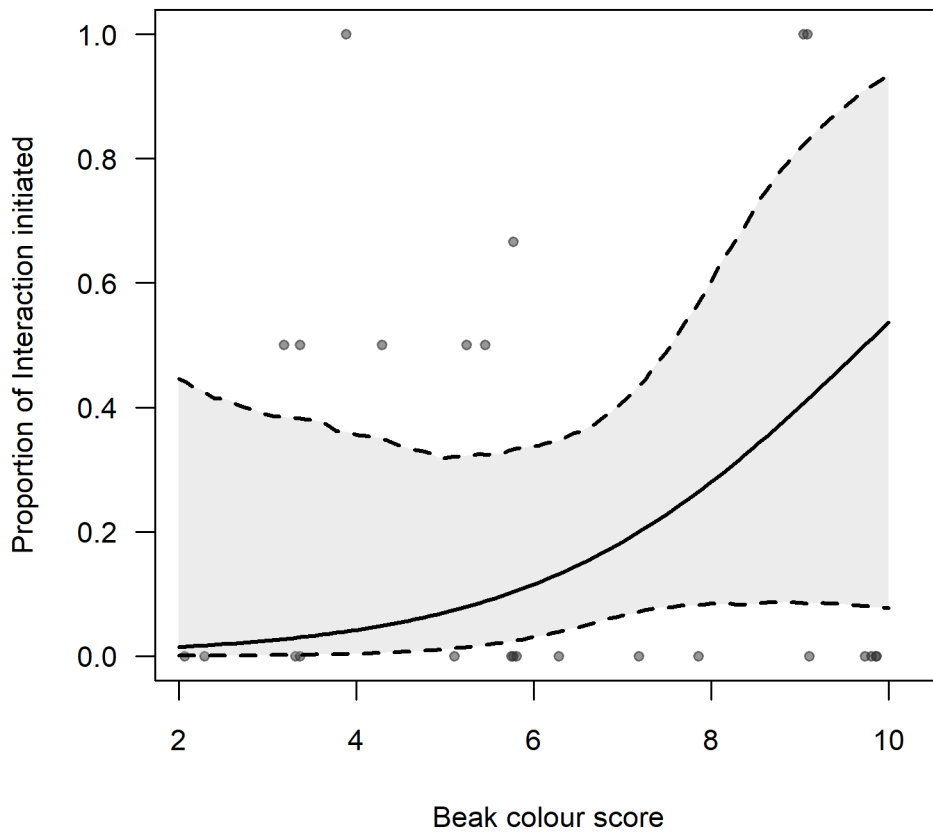


Figure 7: The correlation between the proportion of interactions an individual initiated and its beak colour, corrected for day in year. The regression line is based on a binomial model. Upper and Lower limit of the 95% credible interval are indicated with dashed lines. n=25

Appendix A



Example of a split screen video. Two recordings run simultaneously (time indication at the bottom of the picture). The two food patches are labelled with "Food 1" and "Food 2". The code "2a" or "2B" indicates the number of the video session and the name of the camera used.

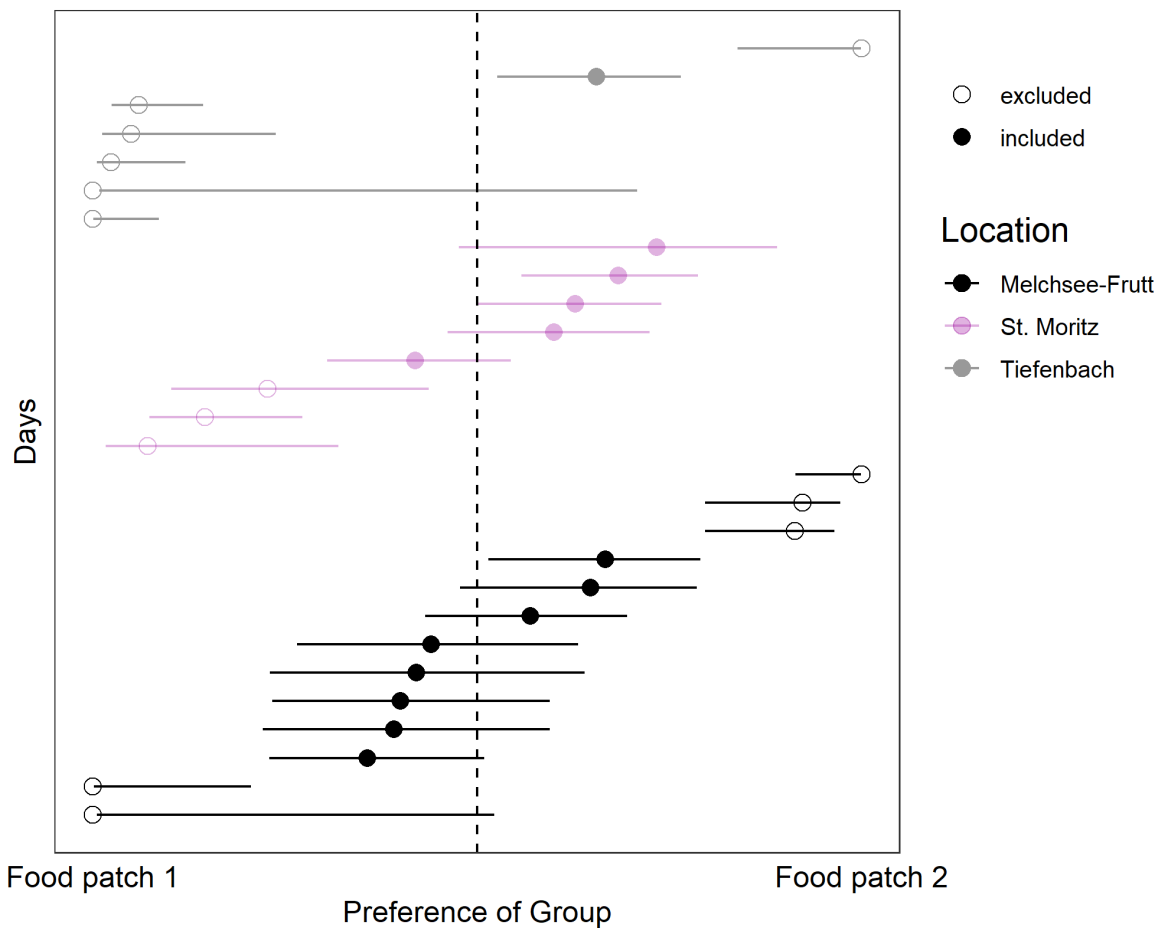
Appendix B

Code	Description	Category
Fight	Two snowfinches jump towards each other, pointing beaks and feet at each other and flapping their wings. Both are actively and passively involved in the interaction	Physical contact
Arched back	The active snowfinch turns against conspecific, puts up the back feathers (arches its back) and keeps head and wings low. It often opens the beak. The conspecific can react in two ways 1) it behaves passively by running away or 2) it becomes active and starts a counterattack	No physical contact
Pecking	The active snowfinch turns against conspecific, jumps, or runs towards it and pecks it with the beak, sometimes it tries to pull out feathers of the conspecific. The conspecific can react in two ways 1) it behaves passively by running away or 2) it becomes active by pecking back	Physical contact
Chase	The active snowfinch runs or flies after a conspecific, opens its beak and tries to peck the conspecific (often multiple times). The conspecific runs away until... 1) the active snowfinch stops chasing it 2) the conspecific stops, turns around and becomes active by pecking back	No physical contact
Jump	The active snowfinch jumps on the back of the conspecific (passive)	Physical contact

Ethogram for agonistic behaviours: Describes how the active (attacking) individual and the passive (attacked) individual behave in interactions. It is unclear under what conditions the snowfinches display which behaviour; however, we assume that all behaviours listed here are related to rivalry and competition.

Appendix C

Positions of the two food patches, provided for snowfinches, varied from day to day. Depending on tourism, we had to place the patches further away from slopes or infrastructure. These spatial shifts may have altered distances to perching sites or niches, where snowfinches can find shelter. Food patches close to retreats could be preferred due to minimised predation risk (Tsurim et al. 2008 and 2010). To account for any preferences for food patch positions in our analyses, we calculated a daily preference value for both patches based on how they were used by snowfinch groups. Every 20 s of a video, we compared the number of snowfinches at one patch with the number at the other patch. The food patch with the most birds got a preference point. If there were equal numbers of birds at both feeders, no point was given. Then we divided the sum of the preference points that each patch received on a field day by the total number of points given. The results were the daily preference values for the two food patches (Numbers between 0 and 1). We made different numbers of videos per field day and observed different numbers of snowfinch groups, why we specified a 95% credible interval for the preference values. We used a beta distribution as prior distribution and calculated 2.5% and 97.5% quantiles. For estimating splitting probability of snowfinch groups (see Methods), we excluded the data of field days, where we got a preference value smaller than 0.25 for one of the food patches (see figure below).



Daily preference of snowfinch groups for food patch positions (to distinguish the two patches, they are randomly labelled as 1 or 2): The points correspond to the calculated daily preference values for food patch 2 (if this value is below 0.5, i.e., behind the dashed line, this corresponds to a preference for food patch 1). The unfilled circles mark the days that were excluded for the splitting probability analysis. The segments show 95% credible intervals. Field days on the y-axis are not arranged by date, but by preference values and by study sites (Sites are indicated with colours).