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# Effectiveness of virtual fencing in a mountain environment and its impact on heifer behaviour and welfare

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ABSTRACT

Virtual fencing (**VF**) could be beneficial in mountain areas where electric wire fencing is difficult and time-consuming. However, environmental challenges of mountain pastures may impair VF efficacy and functionality, with potential effects on animal behaviour and welfare. Thirty female heifers were equipped with activity sensors and VF collars to record activity behaviour, VF audio tones (**AT**s) and electric pulses (**EP**s). After VF training in the lowlands, the heifers were moved to a Swiss summer pasture. The mountain site was divided into nine paddocks, three of which were fenced with electric wire only (**EF-only treatment**) and six additionally used VF (**VF treatment**). During mountain grazing, the herd was split into three groups of 10 heifers each. All groups grazed simultaneously in separate paddocks and moved sequentially through the nine paddocks in a rotational grazing system. Video cameras recorded animal reactions upon virtual fence contact. Grass height was measured to estimate forage availability in the currently grazed paddocks. Data were analysed using mixed-effects models. From the activity data, we also calculated the Degree of Functional Coupling (**DFC**), a metric for examining circadian activity rhythms as an indicator of longer-term animal welfare, ranging from zero (poor) to one (good state of welfare). Throughout mountain grazing, we recorded 36 escaped animals in 11 events crossing an electric fence and 17 escaped animals in eight events linked to VF. Heifers received a mean (± SD) number of 5.9 ± 8.2 ATs and 0.3 ± 0.8 EPs per day. The ATs and EPs increased at lower grass heights (both $P \leq 0.004$) and on days with unforeseen events (both $P \leq 0.001$), such as encounters with wildlife or neighbouring cattle. Grazing interruptions associated with ATs were shorter during mountain grazing compared to VF training ($P < 0.001$). Fence type did not affect heifer step count ($P > 0.05$), but daily lying time was 10 min longer in the VF than EF-only treatment ($P = 0.001$). The heifer's activity pattern was highly rhythmic at both fence types (DFC ≥ 0.92) but decreased during 7-d periods involving a paddock change within VF treatments ($P < 0.001$). In conclusion, the VF system was as reliable as electric fencing in preventing escape events. Heifers learned to respond appropriately to the VF stimuli, even in challenging mountainous terrain. An overall high activity rhythmicity reflected in the DFC supported that longer-term animal welfare was not compromised by VF use.

## Implications

Virtual fencing uses animal tracking to replace physical boundaries with virtual ones. The technology could be a labour-efficient solution to contain livestock on mountain pastures. However, it was primarily used in open and flat terrain. This is the first study testing virtual fencing efficacy and its impact on animal behaviour and welfare in mountainous conditions. Animals learned to respond appropriately upon virtual fence contact. The technology was as reliable as electric fencing. Therefore, virtual fencing has the potential to facilitate mountain livestock farming practices, promote the use of land ideally suited to grazing livestock, and thereby preserve these valuable ecosystems.

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## Introduction

Rangelands represent 54% of the world's terrestrial surface and serve as a valuable source of forage for both domestic and wild ruminants (ILRI et al., 2021). In Switzerland, one-third of the country's agricultural land is dedicated to mountain pastures (Herzog and Seidl, 2018), which provide a wide range of ecosystem services (Pauler et al., 2024). However, in recent decades, many mountain pastures have been underused or even abandoned due to a lack of agricultural labour, changes in management practices, and high maintenance costs (Herzog and Seidl, 2018). As a result, mountain pastures are undergoing natural reforestation, which is leading to a loss of biodiversity (Zehnder et al., 2020) and multifunctionality (Schils et al., 2022). There is a need for a more labour-efficient solution, and the implementation of virtual fencing (**VF**) in mountainous areas could be a promising prospect (Horn and Isselstein, 2022).

In the present study, a commercially available virtual fencing technology for cattle (Nofence AS, Batnfjordsør, Norway) was used. The technology enables pasture boundaries to be set using a smartphone application, and the animals are equipped with global navigation satellite system collars that communicate via a mobile network. When an animal reaches the predefined virtual boundary, the collar emits an ascending audio tone (**AT**), followed by a mild but aversive electric pulse (**EP**) when crossing it.

Numerous studies have shown that sheep (Marini et al., 2018a; Marini et al., 2018b) and cattle (Verdon et al., 2020; Fuchs et al., 2024) are able to learn the association between AT and EP, and ultimately avoid EPs by turning at the virtual boundary in response to an AT. Similar findings were shown to be consistent across younger and older dairy cows (Confessore et al., 2024). Furthermore, indicators such as activity behaviour, pasture utilisation, herbage consumption, BW, milk yield and cortisol concentrations (Campbell et al., 2019; Verdon et al., 2021a; Hamidi et al., 2022; Fuchs et al., 2024) did not differ between virtually fenced and electrically fenced groups, suggesting comparable outcomes in terms of animal behaviour and welfare across fence types in the above-mentioned studies.

Up to now, VF has been tested primarily in research or purpose-built experimental facilities, flat landscapes, and open areas with well-defined paddocks, mostly in Australia (Lee et al., 2009; Lomax et al., 2019; Campbell et al., 2020; Verdon et al., 2020; Colusso et al., 2021), the United States (Ranches et al., 2021; Boyd et al., 2022; Jero et al., 2025), and Europe (McSweeney et al., 2020; Aaser et al., 2022; Confessore et al., 2022; Hamidi et al., 2022). However, VF could be particularly promising in rough and extensive mountainous areas, where electric wire fencing is difficult and more time-consuming than in lowland areas due to the more challenging environmental conditions. Indeed, mountain pastures are steeper, larger, rockier, with more heterogeneous vegetation of lower forage yield and quality, and weather conditions can be harsher than in lowland pastures. In addition, mountainous regions are also characterised by a higher density of wildlife, which can cause encounters with livestock, thus affecting livestock behaviour. It is thus of interest to investigate whether electric wire fencing and VF are equally effective under mountain conditions.

To the best of our knowledge, there is no scientific data available on the use of VF in mountainous areas. Consequently, there is a lack of information regarding the efficacy of VF in mountainous terrain and its potential impact on animal behaviour and welfare. To fill this knowledge gap, the present study focused on two key objectives: (1) To determine the effectiveness of VF in mountainous conditions within a rotational grazing management system; and (2) to assess the potential impact of VF on cattle behaviour and welfare in a mountain environment.

Related to Objective (1) it was hypothesised that the VF would serve as an effective fencing tool in mountainous terrain. This would be reflected in the animal's ability to adapt to the VF system, even under challenging conditions typical of a mountain pasture. To demonstrate the efficacy, it was predicted that the overall number of EPs would decrease over time, and the heifers would respect the virtual boundaries of their designated grazing area. In relation to Objective 2, to assess animal behaviour and welfare, it was hypothesised that behavioural responses upon virtual fence contact would become increasingly appropriate as learning progressed. It was also hypothesised that there would be no difference in the number of steps and time spent lying by the animals between electric fencing and VF as measured by activity sensors. Moreover, a novel, original approach was used to compare the effect of fence type on animal welfare by looking at rhythmic patterns of heifer locomotor behaviour based on a time series analysis. Rhythmic behavioural patterns can serve as an indicator of animal welfare, responding sensitively to internal (e.g., disease) or external (e.g., distress) disturbances (Wagner et al., 2021). Consequently, the computation of rhythmicity may provide valuable insights into the welfare of animals. The activity rhythmicity can be quantified by the Degree of Functional Coupling (**DFC**), a metric for measuring longer-term welfare in animals (Scheibe et al., 1999; Berger et al., 2003; Nunes Marsiglio Sarout et al., 2018). It was hypothesised that the DFC would be unaffected by fence type and remain overall high, which is supportive of a positive state of welfare.

## Material and methods

### *Animals and sensors*

The study included 32 heifers from a conventional Swiss dairy farm, two of which were used as replacements. Heifers were selected to be representative of common practice in Swiss mountain farming. Indeed, they typically graze on less productive pastures than lactating dairy cows, which further emphasises the importance of testing the VF efficacy with heifers in a mountain environment. The animals were of the following breeds: Holstein Friesian (19 heifers), Montbéliarde (four heifers) and Holstein Friesian × Montbéliarde (six heifers) and Holstein Friesian × Jersey crosses (three heifers). At the beginning of the study, heifers were on average (± SD) 11.9 ± 1.6 months of age. All animals were introduced to electric fencing prior to the experiment, but they were naïve to both VF and grazing in mountain pastures. Each heifer was fitted with a VF collar (Nofence AS, Batnfjordsør, Norway) and a leg-mounted activity sensor (IceQubes, Peacock Technology Ltd., Stirling, UK), both of which remained on the heifers throughout the study.

### *Study area and experimental design*

The experiment was conducted between May and August 2023 in the canton of Vaud, Switzerland. The study comprised two experimental stages: (I) acclimatisation and VF training, and (II) mountain grazing. In both stages, the animals were on pasture all day.

#### *(I) Acclimatisation and virtual fencing training*

All heifers were trained together in a single group on a lowland pasture (about 700 m above mean sea level, 46°35′51.0″N 6°46′36.0″E), the mean temperature was 12.6 ± 1.9 °C per day, with a total precipitation of 26.4 mm throughout 16 d of training, measured at an official weather station located 8 km from the site at a comparable altitude. The training paddock was characterised by flat topography and productive pastures. It was divided into two paddocks (**T1** and **T2**) with their outer perimeters delimited by a double-wire electric fence of about 6 kV (Supplementary Figure S1). Inside the paddocks, a straight virtual fence line was placed parallel to an outer electric fence at a distance of about 12 m. After a few days, a second perpendicular virtual fence line was added. The training procedure was designed in several small sub-steps over a total of 16 d to facilitate animal learning (Supplementary Figure S1). It was adopted from Hamidi et al. (2022), where it was shown to be effective for VF training. Additionally, the animals were trained to change from T1 to T2 to test their learned skills in a new setting and to ensure sufficient feed availability during the training period.

*(II) Mountain grazing*

On Day 17 of the experiment, thirty heifers were transported to a mountain summer pasture in the Swiss Pre-Alps (between 1 300 and 1 500 m above mean sea level, 46°30′31.0″N 7°11′17.0″E). Mean temperature was 13.3 ± 3.1 °C per day and total precipitation was 389 mm throughout mountain grazing, measured at an official weather station at 1 500 m altitude located 14 km from the site. During the study, the mobile network connection was generally good and sufficient for the operation of the VF system. The summer pasture covered 10.2 ha (Table 1) and consisted of a typical mountainous landscape, including some flat and open areas as well as steeper ones with rocks, shrubs and trees. The vegetation was composed by a mosaic of nutrient-rich and nutrient-poor pastures. The area was divided into nine paddocks (P1-9): three were fenced with a double-wire electric fence only (P4-6; **EF-only treatment**) and six included a VF boundary (P1-3 and P7-9, **VF treatment**) on at least two sides of the paddocks and a double-wire electric fence on the remainder (Fig. 1). All electric fences were regularly checked to maintain a voltage of about 6 kV. The size of the nine paddocks was calculated to provide a comparable amount of forage based on the estimated botanical composition and associated pasture productivity and in relation to its slope and proportion of non-grazable areas.

The herd was divided into three groups (A, B, and C) of 10 heifers each, balanced by age and breed and maintained throughout the grazing period. Each group grazed simultaneously but in a separate paddock during nine mountain grazing periods (M1-9). The grazing length per paddock (Table 1) depended on the limiting factor of forage availability and averaged 9 d (min. 7 to max. 14 d). A paddock change took place on the same day for all groups. This procedure was repeated until each of the three groups had grazed each of the nine paddocks once (i.e., 6 replicates of the VF treatment and three replicates of the EF-only treatment per group). During the EF-only treatment, the VF collars remained on the animals for monitoring purposes only. The EF-only paddocks were enclosed within a grazing area whose outermost boundary was

**Table 1**
Grazing management and paddock characteristics during virtual fencing training and mountain grazing of the heifers. Grazing periods during virtual fencing training are indicated as Training Periods 1 and 2, and during mountain grazing, as M1-M9. The treatments are defined as electric fencing (EF-only; paddocks fenced with electric wire only) and virtual fencing (VF; paddocks with an additional virtual fence).

| Experimental stage and grazing periods | Average grass height [mm] [1] | Grass residue height [mm] [2] | Animal group [3] | Grazing duration [days] | Paddock | Size [ha] | Median slope [%] | Treatment | Total length [m] | | Estimated proportion of virtual fence length covered by cameras [%] |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | | | Electric fence | Virtual fence | |
| Virtual fencing training | | | | | | | | | | | |
| Training Period 1 | 103.2 | 60 | herd | 10 | T1 | 1.0 | 11.4 | – | 391 [4] | 265 [4] | 100 |
| Training Period 2 | 84.7 | 59 | herd | 6 | T2 | 0.5 | 13.5 | – | 178 [4] | 172 [4] | 100 |
| Mountain grazing | | | | | | | | | | | |
| M 1 | 83.9 | 74 | A | 9 | P1 | 1.1 | 37 | VF | 265 | 180 | 56 |
| M 4 | 74.5 | 71 | C | 9 | | | | | | | |
| M 7 | 61.7 | 53 | B | 14 | | | | | | | |
| M 2 | 70.0 | 63 | A | 7 | P2 | 1.6 | 59 | VF | 193 | 286 | 32 |
| M 5 | 59.3 | 52 | C | 10 | | | | | | | |
| M 8 | 64.6 | 46 | B | 7 | | | | | | | |
| M 3 | 67.0 | 66 | A | 10 | P3 | 1.6 | 49 | VF | 411 | 266 | 26 |
| M 6 | 62.8 | 58 | C | 9 | | | | | | | |
| M 9 | 58.4 | 51 | B | 7 | | | | | | | |
| M 4 | 70.6 | 63 | A | 9 | P4 | 0.9 | 39 | EF-only | 573 | – | – |
| M 7 | 69.7 | 57 | C | 14 | | | | | | | |
| M 1 | 45.3 | 33 | B | 9 | | | | | | | |
| M 5 | 76.2 | 73 | A | 10 | P5 | 0.4 | 23 | EF-only | 304 | – | – |
| M 8 | 75.0 | 72 | C | 7 | | | | | | | |
| M 2 | 51.1 | 39 | B | 7 | | | | | | | |
| M 6 | 68.6 | 67 | A | 9 | P6 | 1.6 | 55 | EF-only | 674 | – | – |
| M 9 | 62.6 | 55 | C | 7 | | | | | | | |
| M 3 | 55.8 | 49 | B | 10 | | | | | | | |
| M 7 | 93.1 | 83 | A | 14 | P7 | 0.9 | 35 | VF | 519 | 152 | 72 |
| M 1 | 80.4 | 66 | C | 9 | | | | | | | |
| M 4 | 60.0 | 44 | B | 9 | | | | | | | |
| M 8 | 77.8 | 65 | A | 7 | P8 | 1.1 | 47 | VF | 322 | 103 | 78 |
| M 2 | 63.2 | 56 | C | 7 | | | | | | | |
| M 5 | 55.0 | 49 | B | 10 | | | | | | | |
| M 9 | 40.0 | 36 | A | 7 | P9 | 1.0 | 55 | VF | 422 | 199 | 50 |
| M 3 | 50.4 | 41 | C | 10 | | | | | | | |
| M 6 | 38.8 | 36 | B | 9 | | | | | | | |

[1] Daily values averaged over grazing time, including values from extrapolation.
[2] Values based on extrapolating the last grazing day within each paddock of the corresponding grazing period.
[3] n = 32 (herd), n = 10 each (Groups A, B, and C).
[4] Length [m] averaged over experimental days by training sub-steps.

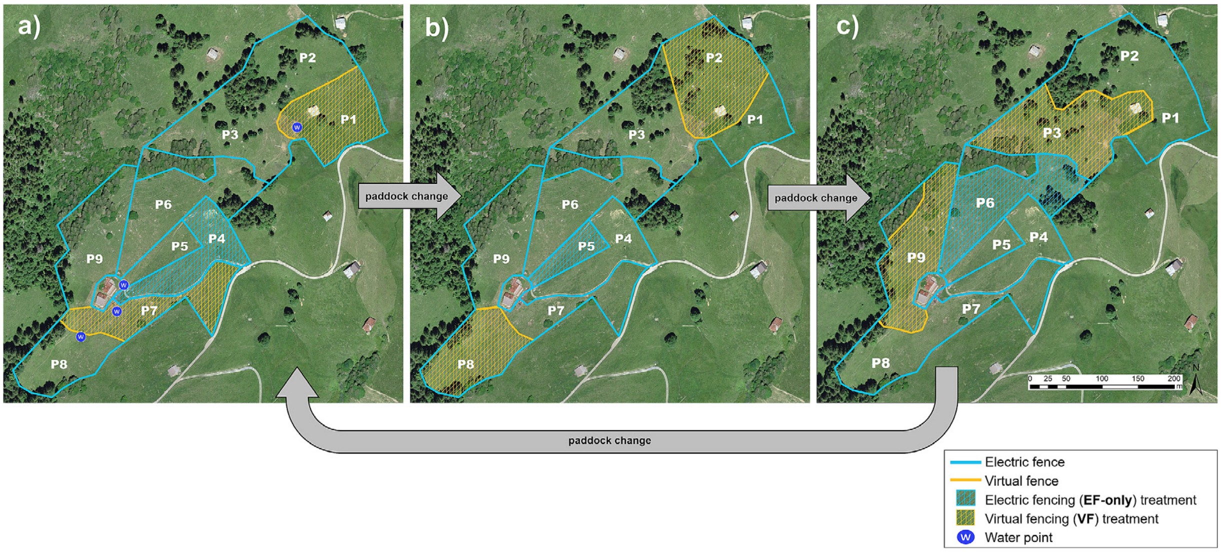

**Fig. 1.** Paddocks of the mountain summer pasture. The outer perimeter of the mountain site was delimited by electric wire fences. The area was divided into nine paddocks. Three of these paddocks were fenced with a double-wire electric fence only (Paddocks 4–6; EF-only treatment) and six included a virtual boundary on at least two sides of the paddocks and a double-wire electric fence on the remainder (Paddocks 1–3 and 7–9, virtual fencing (VF) treatment). Each group of heifers passed successively through each of the 9 paddocks once, grazing separated but simultaneously in (a) Paddocks 1, 4 and 7; (b) Paddocks 2, 5 and 8; and (c) Paddocks 3, 6 and 9, as indicated by the hatched areas. The water supply within the VF treatment was strategically positioned to serve three paddocks in operation during each replicate phase. This approach proved beneficial in a context of limited water access and offered a practical solution from a labour management perspective.

defined by an operational virtual fence located well outside the experimental site to protect the EF-only treatment from receiving VF stimuli in case of positioning signal drift. This was done in a similar manner to complete the polygons of the VF paddocks that were electrically fenced.

### *Data collection and processing*

The data set included recordings of ATs and EPs, behavioural observations, and grass height measurements, which were analysed for both experimental stages – VF training (Days 1–16) and mountain grazing (Days 18–98). Day 17 and Day 99, when animals were transported to and from summer pasture, were excluded from data analysis. The activity behaviour and rhythmicity variables were analysed solely for the mountain grazing period. During mountain grazing, one heifer (group B) was diagnosed with *pneumonia* and was therefore temporarily excluded from the trial (11 d during VF treatment) until full recovery.

### *Paddock characteristics*

To determine the size and slope of each paddock, the polygons of the VF paddocks recorded by the VF system were projected onto the Swiss national coordinate system CH1903+ LV95. The polygons of the EF-only paddocks were measured in the field using a smartphone with global navigation satellite system function and then imported into the grid. This provided the basis for calculating the area and individual fence lengths of the paddocks. In addition, we extracted the median paddock slope of each paddock using the R package “terra” (Hijmans et al., 2024).

### *Number of audio tones and electric pulses and virtual fencing escapes*

The animals were equipped with Nofence collars containing global navigation satellite system for individual positioning at 1-min intervals. If an animal reached the predefined virtual boundary, the collar emitted a rising AT. The AT was terminated when the animal either turned to its designated grazing area or crossed the virtual fence. When crossing, the AT was followed by an EP (0.2 J for 1 s). When the animal remained outside the virtual perimeter, the sequence of stimuli (AT followed by EP) was repeated two more times at the same intensity until it was automatically deactivated. At this point, the animal was classified as an escape (VF escape). The ATs and EPs were maintained in an inactive state until the animal returned to the designated grazing area. Upon the animal’s return and crossing of the virtual boundary from the excluded to the included grazing area, no stimulus was applied.

The VF collars recorded each AT, its duration (in ms) and EP with a georeferenced timestamp. For the training period, the experimental days were defined as a 24-h window from 08:00:00 to 07:59:59 of the following day, as this was the regular time for initiating the steps of the training procedure. Regarding mountain grazing, the original time slot, from midnight to midnight, was maintained. In order to assess the progress of animal learning, we calculated a success ratio based on the methodology published by Hamidi et al. (2024): $Success\ Ratio\ (SR) = \frac{AT_{(excl.\ those\ terminated\ by\ an\ EP)} - EP}{AT}$

The success ratio provides an indication of the animal’s ability to adapt to the VF system. The success ratio quantifies the amount of successful AT, i.e., the extent to which the animal responds correctly to an AT in order to avoid an EP.

### *Escapes associated with electric fences*

During mountain grazing, we documented events of animals escaping from their designated enclosure by crossing an electric fence, hereafter referred to as EF escapes. An EF escape event was identified when heifers were found in a paddock other than their designated paddock and no escape was registered by the VF collars, indicating that the animals had crossed an electric fence to do so. Thus, EF escapes were reported when heifers crossed either an electric fence of the EF-only paddocks or an outer electric fence of the VF paddocks (Table S1). For each EF escape event, the number of animals involved was recorded.

### *Activity behaviour*

The IceQube activity sensors continuously recorded animal leg movements based on 3-axis acceleration with a fixed data sampling rate of 4 Hz and a reporting granularity of 15 min. Records included variables such as step count and lying time which were used for further analysis on a daily basis for each heifer. Due to loss or malfunction, the final dataset contained records of 25 activity sensors during 81 d of mountain grazing. Outliers in activity behaviour were detected using actograms, which reflect the daily activity and resting periods of the animals. In this way, oestrus events were identified as potential confounding factors in the analysis of heifers' activity behaviour. The events were considered as heat events if they met two criteria: (1) the heifer moved continuously for 8 h without resting, represented by a step count >0, and (2) the total number of steps per day exceeded 1.5 times the individual mean step count. Oestrus events were considered as a binary variable in the data analysis. Days on which heifers were classified as being in heat were coded as "1″ and the remaining days were coded as ″0″. Overall, we recorded 67 d of heat events during mountain grazing (representing 3.4% of all experimental days), with 26 d during EF grazing and 41 d during VF grazing. Heat events were recorded in 20 different heifers, some of which were in heat more than once.

### *Rhythmicity in activity patterns*

The present study used the DFC as a supportive tool to evaluate the long-term effects of VF in heifers, extending the scope beyond the more immediate impacts observed in the behavioural reactions or changes in step count or lying time. The DFC quantifies the extent and strength of synchronisation in organisms within a 24-h (circadian) cycle and therefore expresses the harmonic synchronisation with the periodicity of the environment. It identifies significant harmonic periods, defined by dividing 24 h by an integer, resulting in periods of 24, 12, 8 h, and so on (Fuchs et al., 2022). The sum of significant harmonic periods is reflected as a harmonic part in the DFC. Frequencies that are not divided by integers represent nonharmonic periods.

The DFC can take values from 0 to 1. A value of 0 indicates the presence of significant, nonharmonic frequencies only, which is indicative of a de-synchronisation of the organism with the 24-h cycle. Conversely, a DFC of 1 indicates the presence of significant, harmonic frequencies only, which is indicative of a high synchronisation and, thus, a positive state of welfare (Scheibe et al., 1999; Berger et al., 2003; Nunes Marsiglio Sarout et al., 2018). The absence of any significant periods, both harmonic and nonharmonic, implies a lack of rhythmicity and results in the DFC not being computable. The DFC was calculated with the R package "digiRhythm" (Nasser et al., 2022) according to the method described in Fuchs et al. (2022). The sampling interval was based on the 15-min records of individual step count, which were processed over a 7-d sliding window (Day 1 to Day 7, Day 2 to Day 8, etc.) across the duration of 81 d of mountain grazing.

### *Behavioural reactions*

Heifer responses at the virtual boundary were documented using 15 wildlife cameras (Braun Photo Technik GmbH, Scounting Cam Black 1 300, Eutingen, Germany) along the virtual fences. Upon detecting movement, the cameras recorded video sequences in full audio for a preset duration of 2 min. Nighttime recording was possible due to the cameras' IR LEDs (wavelength 850 nm). At least every 3 days, the cameras were manually tested for functionality, the batteries were changed, and the set time was checked for accuracy using an internet-connected smartphone.

During VF training, the full length of the activated virtual fences was covered. During the period of mountain grazing, the cameras were positioned along the activated virtual fences surrounding the water troughs in the respective paddocks. It was assumed that this area would be most frequently visited by the animals, making it the best location for recording virtual fence contacts. An estimated percentage of the virtual fence length covered by the cameras is shown in Table 1.

A total of 1 009 videos were recorded throughout the study. The videos were filtered to include only those animal reactions that were clearly recognisable (e.g., not hidden by other animals or objects). The reactions were then either assigned to an AT or EP based on their timestamps corresponding to a heifer in closest proximity to the virtual boundary within the paddock where the camera was recording at that moment. After verification, 259 videos were identified for further analysis, containing 502 observations (76% related to an AT; 24% related to an EP). Furthermore, observations were alternatively attributed to target animals (in 66% of the cases) or to herd animals (in 34% of the cases). A target animal was defined as an animal exposed to an AT or EP, whereas a herd animal was defined as an animal a target animal receiving a stimulus (e.g., head and ear position directed towards the target animal).

The videos were analysed by a single person using the open-source software "BORIS" (Version 7.12.2; Friard and Gamba (2016)). For each AT and EP observed, individual responses per target or herd animal were documented. Each response could include various behaviours, as listed and individually described in the ethogram in Table 2. In total, nine different behaviours were classified: run (i.e., turn and run away), retreat (i.e., turn and walk away), stay (i.e., turn but keep position), bucking, head shaking, vocalisation, regrazing (i.e., start to graze again), freezing (i.e., staring without any movement), and no reaction. Since head shaking, bucking, vocalisation, and no reaction were recorded in low numbers throughout the experiment (see Supplementary Figure S2), they were excluded from the statistical analysis.

### *Grass height*

Throughout the experiment, grass height was measured to assess forage availability and thus to decide the timing of paddock change. We used a semi-automated electronic rising plate meter (Grasshopper II, TrueNorth Technologies, Ireland), which captured the distance of a plate lift at compressed sward height (in mm) (Hart et al., 2022). Samples were taken every 10 steps by walking in a W-shaped pattern. During VF training, measurements were taken on days when the sub-steps were performed. During mountain grazing, measurements were taken every third and last day of grazing in each of the currently grazed paddocks. In order to complete the grass measurement time series in both experimental stages, a linear extrapolation of the grass height was performed for each paddock using the "approxExtrap" function of the R package "Hmisc" (Harrell and Dupont, 2023).

### *Unforeseen events*

Unforeseen events with a marked effect on animal behaviour were noted to control for possible confounding effects on the number of ATs, EPs and escapes as well as on the activity behaviour and rhythmicity of the heifers. The events included technical (e.g., collar replacement, defective electric fence) and management-related difficulties (e.g., paddock change), as well as unforeseen environmental influences, such as the presence of wildlife (i.e., lynx, deer) or a neighbouring cow herd. In total, we documented 8 different types of unforeseen events that occurred on 16 d throughout the study, affecting 3 d during VF training and 13 d during mountain grazing (Supplementary Table S1). Unforeseen events were considered a binary variable in the data analysis. Each day on which an event occurred was categorised as a "1″ among individuals of the corresponding group, and as a ″0″ if no event occurred. To ensure consistent analysis of the heifers' adaptation process to VF, data cleaning was performed for the number of ATs, EPs, and VF escapes at two specific events related to a paddock change (Supplementary Table S1). The activity data associated with these events were not

**Table 2**
Ethogram of behaviours exhibited by heifers in response to an audio tone (AT) or electric pulse (EP). The hypotheses are based on the assumption that the heifers become more experienced in virtual fencing over time. Point events are indicated by a single occurrence, while status events are indicated by a duration (in s). The checkmarks in the exclusion matrix represent mutually exclusive behaviours. In the context of regrazing and freezing as state events, a regrazing event may be interrupted by freezing. However, the reverse sequence was mutually exclusive.

| | Exclusion Matrix | | | | | Ethogram | | |
|---|---|---|---|---|---|---|---|---|
| Behaviour | Run | Retreat | Stay | Regrazing | Freezing | Response Type | Definition | Hypotheses |
| Run | | x | x | | X | point | Heifer turns around and runs away at trot or canter for at least 1 body length, but stays inside the inclusion zone. | The ratio of Run per AT or EP decreases. |
| Retreat | x | | x | | X | point | Heifer turns around and walks away for at least 1 body length, but stays inside the inclusion zone. | The ratio of Retreat per AT or EP increases. |
| Stay | x | x | | | X | point | Heifer turns around and keeps its position close to the virtual boundary. | The ratio of Stay per AT or EP increases. |
| Bucking | | | | | X | point | Both or at least one hind leg of the heifer lifts off the ground and is kicked backwards at any speed (walk, trot or canter). | The ratio of Bucking per AT or EP decreases. |
| Head shaking | | | | | X | point | Heifer is shaking its head. | The ratio of Head Shaking per AT or EP decreases. |
| Vocalisation | | | | | X | point | Any type of vocalisation. Vocalisations are recorded for each individual call. | The ratio of Vocalisation per AT or EP decreases. |
| Regrazing | | | | | | point + state | Heifer raises its head and stops to graze (start event) until starting to graze again (end event). Grazing = The heifer's head is lowered to the ground while standing or moving. | The duration to start grazing again decreases per AT or EP. |
| Freezing | x | x | x | x | | point + state | Heifer stops moving forward and remains in position with its head raised and directed towards the virtual boundary (start event) until showing an action again (end event). | The freezing time per AT or EP decreases. |
| No Reaction | x | x | x | x | X | point | Heifer does not react at all to the stimuli.<br>e.g., changing in its current behaviour. | The heifers frequently react to ATs to avoid receiving EPs. |

cleaned because the animals ultimately received ATs and EPs, with possible effects on stress levels affecting activity behaviour and rhythmicity.

### *Statistical analyses*

All statistical analyses and figures were performed in R Version 4.2.3. Linear mixed effects models (**LMERs**) and Generalised mixed effects models (**GLMMs**) were fitted according to the distribution of the dependent variables, which were previously checked using histograms, QQ plots, and box plots. LMERs were used to analyse the mean warning duration per AT per day for both experimental stages, as well as the step count and lying time per heifer per day during mountain grazing. The model structure related to the warning duration per AT per day is listed in Supplementary Table S2 (VF training) and Table 3 (mountain grazing). The models for step count and lying time included fence type (VF treatment vs EF-only treatment), paddock size, and median paddock slope as fixed effects. Animal identity within animal group was considered a nested random effect, and experimental days as a crossed random effect. All LMERs were computed using the R package "lme4″ (Bates et al., 2015) on a maximum likelihood structure. The model predictors were tested as main and interaction effects and were selected by backward elimination in a bootstrap test using the R package ″pbkrtest" (Halekoh and Højsgaard, 2014).

The recordings of ATs and EPs per heifer per day and heifer reactions upon virtual fence contact were analysed for both experimental stages using GLMMs with a negative binomial likelihood. Model structures related to the VF stimuli are listed in Supplementary Table S2 (VF training) and Table 3 (mountain grazing) and related to heifer reactions in Table 4. The DFC per heifer was analysed for the mountain grazing period. As DFC is a continuous parameter with values between 0 and 1, a GLMM with an ordered beta likelihood was used. The DFC models included grazing period, fence type (VF treatment vs EF-only treatment only within 7-d period) and paddock change (no vs yes within 7-d period) as fixed effects and animal identity within animal group as nested random effect. All GLMMs were computed using the package "glmmTMB" (Brooks et al., 2017). The model predictors were tested as main and interaction effects and were selected by model comparisons using chi-squared test statistics obtained from a likelihood ratio test. Level of significance was set at 0.05 for all LMERs and GLMMs. To account for potential confounding effects on heifer step count, lying time, and DFC, we tested the occurrence of unforeseen events, average daily grass height, and days in heat as fixed effects in the corresponding models. Furthermore, the impact of unforeseen events treated as a fixed effect and animal group as a random effect was examined in the ATs and EPs models (Table 3). Finally, the selected LMERs and GLMMs were tested for goodness of fit of the simulated residuals using the R package "DHARMa" (Hartig, 2024), including tests for distribution, over/ under-dispersion, outliers, and zero inflation.

A Fisher's exact test was used to determine if there was a significant relationship between fence type and the proportion of escapes during mountain grazing. Fisher's exact test was performed in R using the fisher.test() function. Two sample sizes were evaluated: on a daily basis, we used 81 days of mountain grazing for both treatments; and on an individual level, we used 81 days of mountain grazing × 10 animals × 2 (VF treatment) or 3 (EF treatment) replicates because each of the three groups used electric fencing, but only two groups used VF. At the individual level, escaped animals were treated as independent data points, assuming that each individual would escape only once per day. The significance level was set at 0.05.

## Results

### *Audio tones, electric pulses and escapes*

#### *(I) Virtual fencing training*

Heifers received a mean number of 14.9 ± 26.8 ATs and 1.4 ± 1.8 EPs per day (Supplementary Table S2). This represents a daily ratio of 0.15 ± 0.20 EP per AT. The mean warning duration was 7.1 ± 6.4 s per AT, with ATs being terminated after 3.4 ± 4.9 s for heifers returning to pasture and after 9.6 ± 4.8 s for heifers receiving an EP. During VF training in paddock T1, the frequency of EPs followed

**Table 3**
Summary output of the generalised mixed-effects models (GLMMs) analysing audio tone and electric pulse records, as well as the output of the linear mixed-effects model (LMER) analysing the warning duration during the heifers' mountain grazing. Model predictors were either numeric, such as grazing periods, days after paddock change (DPC) and average grass height, or categorical, such as the occurrence of unforeseen events (yes or no). Numeric predictors were tested as main and interaction effects, and the categorical predictor was tested as a main effect only.

| Dependent variable | N ($N_{days} \times N_{animals}$)[1] | Mean | SD | Random effects | Model predictors | Estimated Coefficient | 95% Confidence interval (CI) | | *P*-value ($\alpha = 0.05$)[2] |
|---|---|---|---|---|---|---|---|---|---|
| | | per heifer and day | | | | | lower CI | upper CI | |
| Audio tones [AT count] | Group A & C: (54 ×20) + Group B: (56 ×10) | 5.9 | 8.2 | Heifer ID nested in Group + Experimental days | Period | – 0.477 | −0.82 | −0.14 | 0.006 ** |
| | | | | | DPC | – 0.528 | −0.94 | −0.12 | 0.012 * |
| | | | | | Grass height | – 0.042 | −0.07 | −0.02 | 0.001 ** |
| | | | | | Period ×DPC | 0.109 | 0.03 | 0.19 | 0.007 ** |
| | | | | | Period ×Grass height | 0.006 | 0.00 | 0.01 | 0.016 * |
| | | | | | DPC ×Grass height | 0.007 | 0.00 | 0.01 | 0.013 * |
| | | | | | Period ×DPC ×Grass height | – 0.002 | 0.00 | 0.00 | 0.014 * |
| | | | | | Event yes [baseline level: no] | 0.602 | 0.31 | 0.89 | < 0.001 *** |
| Electric pulses [EP count] | Group A & C: (54 ×20) + Group B: (56 ×10) | 0.3 | 0.8 | Heifer ID nested in Group + Experimental days | Period | −1.315 | −2.33 | −0.31 | 0.011 * |
| | | | | | DPC | −1.052 | −2.01 | −0.10 | 0.031 * |
| | | | | | Grass height | −0.091 | −0.15 | −0.03 | 0.004 ** |
| | | | | | Period ×DPC | 0.316 | 0.10 | 0.53 | 0.003 ** |
| | | | | | Period ×Grass height | 0.021 | 0.01 | 0.04 | 0.010 * |
| | | | | | DPC ×Grass height | 0.018 | 0.00 | 0.03 | 0.011 * |
| | | | | | Period ×DPC ×Grass height | −0.005 | 0.00 | 0.00 | 0.002 ** |
| | | | | | Event yes [baseline level: no] | 1.305 | 0.74 | 1.87 | < 0.001 *** |
| Warning duration [s per AT] | Group A & C: (54 ×20) + Group B: (56 ×10) | 4.5 | 3.0 | Heifer ID nested in Group + Experimental days | Period | −0.422 | −0.96 | 0.10 | 0.234 |
| | | | | | DPC | −0.244 | −0.84 | 0.36 | < 0.001 *** |
| | | | | | Grass height | −0.037 | −0.07 | 0.00 | 0.294 |
| | | | | | Period ×DPC | 0.115 | 0.00 | 0.23 | 0.564 |
| | | | | | Period ×Grass height | 0.006 | 0.00 | 0.01 | 0.898 |
| | | | | | DPC ×Grass height | 0.009 | 0.00 | 0.02 | 0.391 |
| | | | | | Period ×DPC ×Grass height | −0.002 | 0.00 | 0.00 | 0.037 * |
| | | | | | Event yes [baseline level: no] | 0.115 | −0.44 | 0.74 | 0.632 |

[1] Excluding $N_{days}$ with deactivated virtual fence and transportation of the heifers to (Day 17) and from (Day 82) the mountain summer pasture.
[2] Significance levels indicated by $P < 0.001$ (***), $P < 0.01$ (**), $P \leq 0.05$ (*).

a zigzag trend characterised by an increase on the days when the training sub-steps were performed and a decrease on the following days (Fig. 2). This trend was no longer observed after the heifers were moved to paddock T2. The overall success ratio was 69.0 ± 3 8.3%, with an increase from 62.1 ± 40.1% in the first period to 80.4 ± 32.0% in the second period (Table 5). Following the initial VF activation on experimental Day 2, the success ratio increased by approximately twofold after 3 days of VF experience. The mean number of ATs and EPs reached a peak on experimental Day 10 (Fig. 2), which was the last grazing day in paddock T1 and on which a feed shortage was documented due to rainy weather conditions with a lot of grass trampled and muddied by livestock (Supplementary Table S1). On this day, the mean number of ATs was about 9 times and the mean number of EPs about 3 times higher than on experimental Day 2, where the VF system was activated for the first time. Despite the overall higher number of ATs and EPs on experimental Day 10, the success ratio was at 75.5 ± 18.1%, representing a higher level than the period average (Table 5).

When the heifers were moved to paddock T2, the ATs and EPs decreased to a lower number (Fig. 2). Additionally, the success ratio reached its highest level (≥ 90%) from experimental Days 12–14 (Table 5). Then, the ATs and EPs increased again on experimental Day 15 (Fig. 2). There were nine escapes recorded throughout the training period. On experimental Day 15, the three recorded escapes contributed to the higher number of EPs on that day. Three more escapes were linked to the removal of the electric wire on experimental Day 3, two escapes to the paddock change on experimental Day 11 and one escape to the feed shortage on experimental Day 10 (Fig. 2).

As shown by the GLMM, there were significant correlations between the number of ATs and EPs and various model predictors tested (see Supplementary Table S2). Of these, period as a main effect and its interaction with training days and grass height were identified to have the greatest impact related to their estimated coefficients. The number of ATs ($P = 0.041$) and EPs ($P < 0.001$) was likely to increase from training period 1 to training period 2. Moreover, we estimated fewer ATs ($P = 0.002$) and EPs ($P < 0.001$) within training period 2 compared to training period 1 as more training days were completed within the periods. Similarly, the warning duration per AT increased with additional training days throughout the entire training period ($P < 0.001$) but decreased when considering the interaction effect of period and training days ($P < 0.001$). Furthermore, there was a negative correlation between the number of ATs and EPs and the interaction of grass height and grazing periods (both $P < 0.001$). These results suggest that as grass height declined over the course of grazing time within period training period 2, the number of ATs and EPs was likely to increase when compared to training period 1.

### *(II) Mountain grazing*

Heifers received a mean number of 5.9 ± 8.2 ATs and 0.3 ± 0.8 EPs per day (Table 3). This represents a daily ratio of 0.04 ± 0.1 EP per AT. The mean warning duration was 4.5 ± 3.0 s per AT and was longer when terminated by an EP than when the animal returned to the pasture (7.3 ± 2.1 s vs 3.8 ± 2.8 s). In periods M1, M4 and M7, the groups changed their management treatment from either EF to VF or vice versa and maintained it for two paddock changes (e.g., M1-3; M4-6; M7-9, see Fig. 2). The rotation of treatments is reflected in the total number of ATs and EPs shown in Table 5, which were particularly high in periods M1 and M2 compared to M3, and higher in M4 and M5 compared to M6 (with shorter or even comparable grazing duration per paddock, respectively). Groups did not differ in the number of ATs ($P = 0.999$) and EPs ($P = 0.860$) as well as in the warning duration per AT

**Table 4**

Summary output of the generalised mixed-effects models (GLMMs) to analyse heifer responses upon virtual fence contact by stimuli type (AT = audio tone vs EP = electric pulse), animal subject (target vs herd animal) and experimental stage (T = training vs MG = mountain grazing). All model predictors were categorical. They were tested as main effects for each dependent variable, as well as for interaction effects on regrazing time and freezing time.

| Dependent variable | Mean | SD | Random effects | Model predictors | Estimated Coefficient | 95% Confidence interval (CI) | | *P*-value ($\alpha = 0.05$) [1] |
|---|---|---|---|---|---|---|---|---|
| | per observed AT / EP per video | | | | | lower CI | upper CI | |
| Run [count] | 0.01 / 0.35 | 0.13 / 0.50 | Total heifers seen in video + Video ID | Experimental stage MG [baseline level: T] | −0.798 | −2.17 | 0.57 | 0.235 |
| | | | | Animal subject herd [baseline level: target animal] | −0.389 | −1.06 | 0.29 | 0.259 |
| | | | | Type of stimuli EP [baseline level: AT] | 3.181 | 2.04 | 4.33 | < 0.001 *** |
| Retreat [count] | 0.76 / 0.82 | 0.44 / 0.51 | Total heifers seen in video + Video ID | Experimental stage MG [baseline level: T] | 0.108 | −0.11 | 0.33 | 0.330 |
| | | | | Animal subject herd [baseline level: target animal] | −0.066 | −0.28 | 0.15 | 0.550 |
| | | | | Type of stimuli EP [baseline level: AT] | 0.122 | −0.12 | 0.37 | 0.332 |
| Stay [count] | 0.25 / 0.00 | 0.44 / 0.00 | Total heifers seen in video + Video ID | Experimental stage MG [baseline level: T] | 0.444 | −0.96 | 0.95 | 0.084 |
| | | | | Animal subject herd [baseline level: target animal] | 0.059 | −0.42 | 0.54 | 0.809 |
| Regrazing time [s] | 8.98 / 13.26 | 8.98 / 8.07 | Total heifers seen in video + Video ID | Experimental stage MG [baseline level: T] | −0.594 | −0.93 | −0.26 | < 0.001 *** |
| | | | | Animal subject herd [baseline level: target animal] | −0.007 | −0.50 | 0.48 | 0.979 |
| | | | | Type of stimuli EP [baseline level: AT] | 0.811 | −0.01 | 1.63 | 0.052 |
| | | | | Animal subject ×Experimental stage | 0.156 | −0.45 | 0.76 | 0.611 |
| | | | | Animal subject ×Type of stimuli | −0.893 | −2.10 | 0.32 | 0.147 |
| | | | | Experimental stage ×Type of stimuli | −0.893 | −2.50 | 1.34 | 0.554 |
| Freezing time [s] | 5.03 / 7.92 | 7.20 / 5.24 | Total heifers seen in video + Video ID | Experimental stage MG [baseline level: T] | −0.756 | −1.83 | 0.32 | 0.167 |
| | | | | Animal subject herd [baseline level: target animal] | 0.179 | 0.70 | 2.88 | 0.001 ** |
| | | | | Type of stimuli EP [baseline level: AT] | 0.732 | −0.05 | 1.51 | 0.066 |
| | | | | Animal subject ×Experimental stage | −0.843 | −2.44 | 0.75 | 0.301 |
| | | | | Animal subject ×Type of stimuli | −1.768 | −3.14 | −0.39 | 0.012 * |

[1] Significance levels indicated by $P < 0.001$ (***), $P < 0.01$ (**), $P \leq 0.05$ (*).

($P = 0.681$). The overall success ratio was at 90.9 ± 22.7% (Table 5). We recorded 17 escaped animals in 8 events linked to VF and 36 escaped animals in 11 events linked to electric fencing (Fig. 2). Fisher's exact test showed that the rate of escape events ($P = 0.626$) and escaped animals ($P = 0.262$) was not related to fence type. In the VF escape events, all heifers returned to their group without human intervention. In the EF escape events, the heifers had to be returned to the correct paddock because they either could not find their way back on their own or had mixed with another group of animals.

The GLMM (Table 3) indicated a decrease in the number of ATs and EPs with grazing periods ($P = 0.006$ and $P = 0.011$, respectively) and days after paddock change ($P = 0.012$ and $P = 0.031$, respectively). Moreover, the warning duration per AT decreased with increasing days after paddock change ($P < 0.001$). Higher grass height significantly reduced the number of ATs ($P = 0.001$) and EPs ($P = 0.004$; Table 3). This effect is further highlighted by the significant interaction of average grass height and days after paddock change. Here, the number of EPs rose considerably over time at overall lower grass heights, as shown in Fig. 3. Furthermore, the number of ATs ($P = 0.001$) and EPs ($P < 0.001$) was higher on days where we documented unforeseen events compared to those days when no such events occurred (Table 3).

### *Animal reactions upon virtual fence contact*

Throughout the experiment, we most frequently recorded run, retreat, stay, regrazing and freezing behaviour (Supplementary Figure S2). The behaviours stay and no reaction were never observed in response to an EP. Bucking, head shaking, and vocalisation were usually associated with an EP, but were generally rare (≤ 0.1 times per AT or EP in each case, Supplementary Figure S2). As shown by the GLMMs in Table 4, heifers ran more frequently after receiving an EP than an AT ($P < 0.001$), while there was no effect of the experimental stage or animal subject. Similarly, the number of retreat and stay did not vary with stimulus type, experimental stage, or animal subject. Furthermore, the frequency of turning around and walking away from the boundary (retreat) in response to an EP increased from training to mountain grazing, whereas the frequency of turning around and running in such situations decreased (Supplementary Figure S2). However, these trends were not significant.

Regrazing and freezing were predominantly recorded during the training period (Supplementary Figure S2). In response to an EP during mountain grazing, regrazing and freezing was never documented, hence the missing box plots in Fig. 4. As shown in Table 4, mean regrazing time decreased from training to mountain grazing ($P < 0.001$). During training, the mean regrazing time for target and herd animals associated with an AT was 11.6 and 12.1 s, and 20.1 and 9.8 s associated with an EP (Fig. 4). Furthermore, mean freezing time was longer for herd than for target animals ($P < 0.001$, Table 4), both during VF training (26.5 vs 3.9 s) as well as during mountain grazing (4.4 vs 1.8 s) (Fig. 4). Conversely, target animals during training remained frozen longer when exposed to an EP compared to herd animals observing (8.5 vs 7.3 s; Fig. 4).

### *Step count and lying time*

During mountain grazing, heifers took a mean number of 3 074 ± 940 steps and spent 630 ± 119 min lying per day. The mean number of steps taken by the animals was not affected by fence type as a main effect ($P > 0.05$). However, the interaction between fence type and mean paddock size or median paddock slope had a significant impact on step count (Fig. 5): Heifers took fewer steps in the VF treatment and more steps in the EF-only treatment at larger paddock sizes ($P < 0.001$) and at an increased paddock slope ($P < 0.001$). Furthermore, the mean lying time per day was about 10 min longer in the VF treatment compared to the EF-only

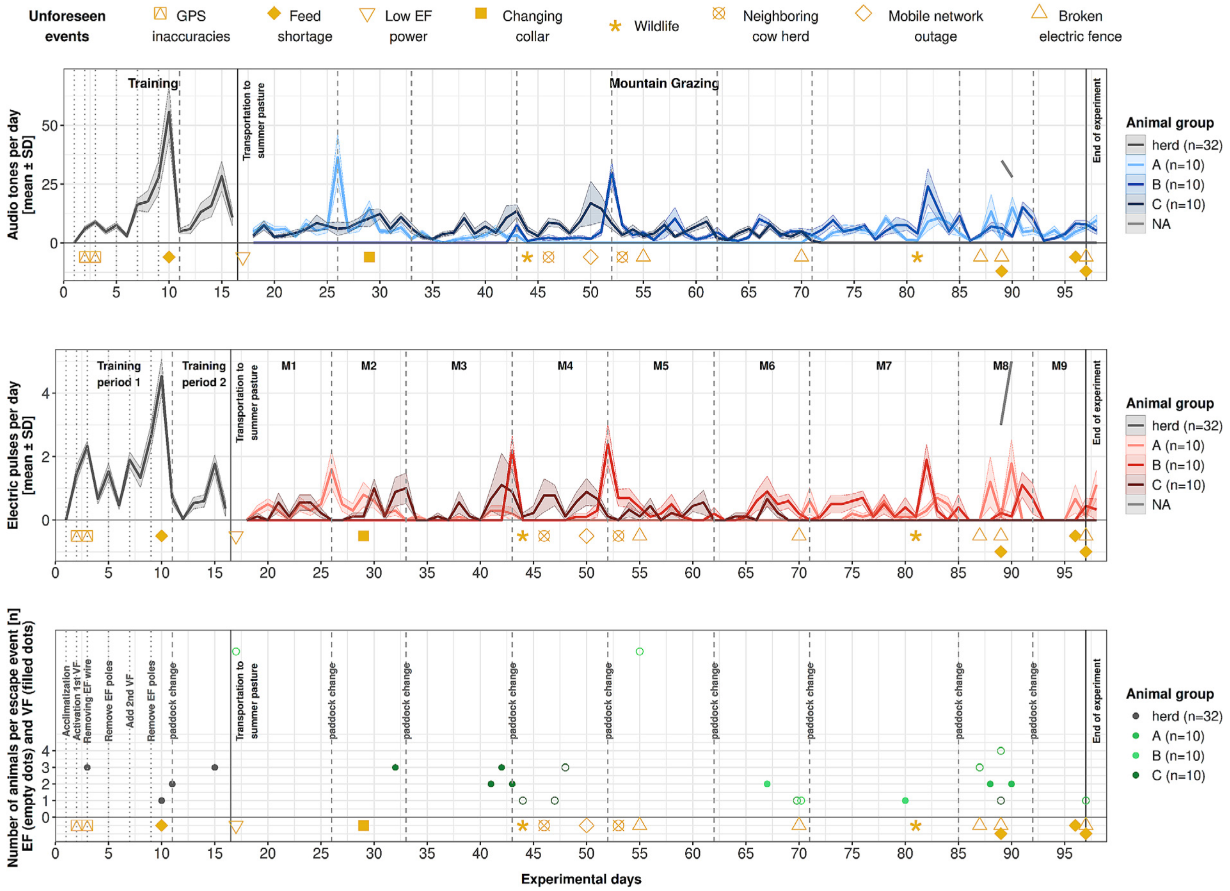

**Fig. 2.** Mean number of (a) audio tones and (b) electric pulses per day per heifer group, as well as (c) the absolute number of escape events when heifers crossed a virtual fence (VF) or an electric fence (EF) in either the EF-only or VF paddocks during training and mountain grazing. The mean is shown as a solid line, and the SD as shading. Training days are shown after reassignment to a 24-h window (from 08:00:00 to 07:59:59 of the following day). Details on the unforeseen events can be found in Supplementary Table S1.

treatment ($P = 0.001$). Fence type in interaction with median paddock slope was negatively correlated with lying time (Fig. 5): The steeper the paddock, the less time animals spent lying in both the VF and EF-only treatment ($P = 0.003$). Moreover, lying time decreased in the EF-only treatment and increased in the VF treatment at larger paddock sizes ($P = 0.01$; Fig. 5). Days with unforeseen events did not affect the mean number of steps ($P = 0.585$) and lying time ($P = 0.110$). However, as expected, the number of steps increased ($P = 0.001$) and lying time decreased ($P = 0.001$) on days when the heifers were classified as being in heat. Moreover, average grass height did not affect the mean number of steps ($P = 0.300$), but lying time decreased with lower grass height ($P < 0.001$).

### Degree of functional coupling

The daily activity level of the heifers was characterised by a pattern with two peaks around 0600 and 1800 h and a slight decline around midday. From around 2100–0300 h, the activity level remained low, reflecting the main resting period of the heifers. This pattern was observed consistently across both fence types (EF-only treatment and VF treatment), although the overall daily average of steps was higher for the VF treatments than the EF-only treatments (Fig. 6). Throughout mountain grazing, the mean DFC was 0.93 ± 0.14 for 7-d periods during which heifers grazed in VF paddocks and 0.92 ± 0.17 for 7-d periods during which they grazed in EF-only paddocks. The mean DFC was 0.93 ± 0.12 for 7-d periods that included grazing with both fence types, with at least 1 and up to 6 grazing days in the VF paddocks. While there was a small difference in the mean DFC across fence types, the LMER indicated that the DFC increased when heifers grazed within the VF treatment compared to the EF-only treatment ($P < 0.001$).

Furthermore, the course of the DFC revealed minor fluctuations during mountain grazing, with the overall level remaining high, both during grazing within the VF treatment and EF-only VF treatment (Fig. 6). However, the DFC level decreased with grazing periods ($P < 0.001$). Furthermore, the DFC was influenced by paddock changes ($P < 0.001$), with higher levels measured during 7-d periods including a paddock change compared to those without. However, the DFC was found to decrease at the interaction of paddock change and fence type ($P < 0.001$), indicating that a paddock change within the VF treatment reduced the DFC. Furthermore, the DFC was found to be lower when the heifers were in heat compared to the 7-d periods that did not include heat events ($P < 0.001$). Therefore, heat events are likely to be a confounding variable affecting the DFC. Unforeseen events during mountain grazing did not lead to any change in the DFC ($P = 0.595$).

## Discussion

### Heifers learned to adapt to virtual fencing in a mountain environment

The heifers were effectively trained in the use of VF in flat paddocks in the lowlands, allowing for a successful transition of their newly acquired knowledge to VF grazing in a mountain environment. This was reflected in a consistent increase in the overall success ratio indicating the progress of learning (Hamidi et al., 2024). The heifers thus understood the functioning of VF, even in challenging mountainous terrain, which supports previous studies on

**Table 5**
Results of the Success Ratio (in %) calculated for each grazing period during virtual fencing training (Training Periods 1 and 2) and mountain grazing (Mountain grazing Periods M1-M9) of the heifers. Additionally, a daily list of the experimental days is provided for the virtual fence training period to outline the training sub-steps (see Supplementary Figure S1) on days 2 (virtual fence activation), 3 (removing electric wire), 5 (removing poles), 7 (activating second virtual fence), 9 (removing poles) and 11 (paddock change). The Success Ratio was calculated according to the formula developed by Hamidi et al. (2024).

| Experimental stage and grazing period | Σ Audio tones | Σ Audio tones terminated by electric pulse | Σ Electric pulses | Success Ratio [1] (mean ± SD) |
|---|---|---|---|---|
| Virtual fencing training | | | | |
| Training Period 1 | | | | |
| Day 2 | 195 | 48 | 48 | 33.2 ± 57.4 |
| Day 3 | 285 | 73 | 73 | 39.2 ± 30.6 |
| Day 4 | 158 | 19 | 23 | 68.2 ± 31.7 |
| Day 5 | 240 | 46 | 49 | 48.6 ± 53.5 |
| Day 6 | 90 | 14 | 14 | 64.7 ± 58.4 |
| Day 7 | 507 | 59 | 59 | 74.2 ± 19.9 |
| Day 8 | 547 | 42 | 43 | 81.9 ± 22.2 |
| Day 9 | 863 | 80 | 82 | 75.2 ± 19.0 |
| Day 10 | 1 753 | 142 | 144 | 75.5 ± 18.1 |
| Total | 4 638 | 523 | 535 | 62.1 ± 40.1 |
| Training Period 2 | | | | |
| Day 11 | 155 | 20 | 21 | 66.2 ± 50.5 |
| Day 12 | 184 | 1 | 1 | 98.5 ± 6.6 |
| Day 13 | 432 | 16 | 16 | 95.1 ± 10.2 |
| Day 14 | 498 | 20 | 20 | 90.5 ± 15.5 |
| Day 15 | 926 | 56 | 57 | 81.3 ± 19.4 |
| Day 16 | 340 | 12 | 11 | 58.6 ± 37.3 |
| Total | 2 535 | 125 | 126 | 80.4 ± 32.0 |
| Total both training periods | 7 173 | 648 | 661 | 69.0 ± 38.3 |
| Mountain grazing | | | | |
| M 1 | 1 035 | 45 | 47 | 90.4 ± 19.9 |
| M 2 | 1 175 | 56 | 62 | 91.1 ± 15.7 |
| M 3 | 811 | 37 | 43 | 90.6 ± 30.7 |
| M 4 | 1 161 | 60 | 74 | 92.1 ± 16.9 |
| M 5 | 1 063 | 51 | 58 | 91.1 ± 20.2 |
| M 6 | 785 | 39 | 42 | 88.4 ± 27.3 |
| M 7 | 1 805 | 85 | 88 | 89.7 ± 27.0 |
| M 8 | 895 | 49 | 51 | 93.6 ± 15.7 |
| M 9 | 613 | 27 | 30 | 93.1 ± 19.2 |
| Total | 9 343 | 449 | 495 | 90.9 ± 22.7 |

[1] $SuccessRatio = \frac{Audiotones_{(excl.\ those\ terminated\ by\ an\ electric\ pulse)} - Electric\ pulses}{Audiotones}$

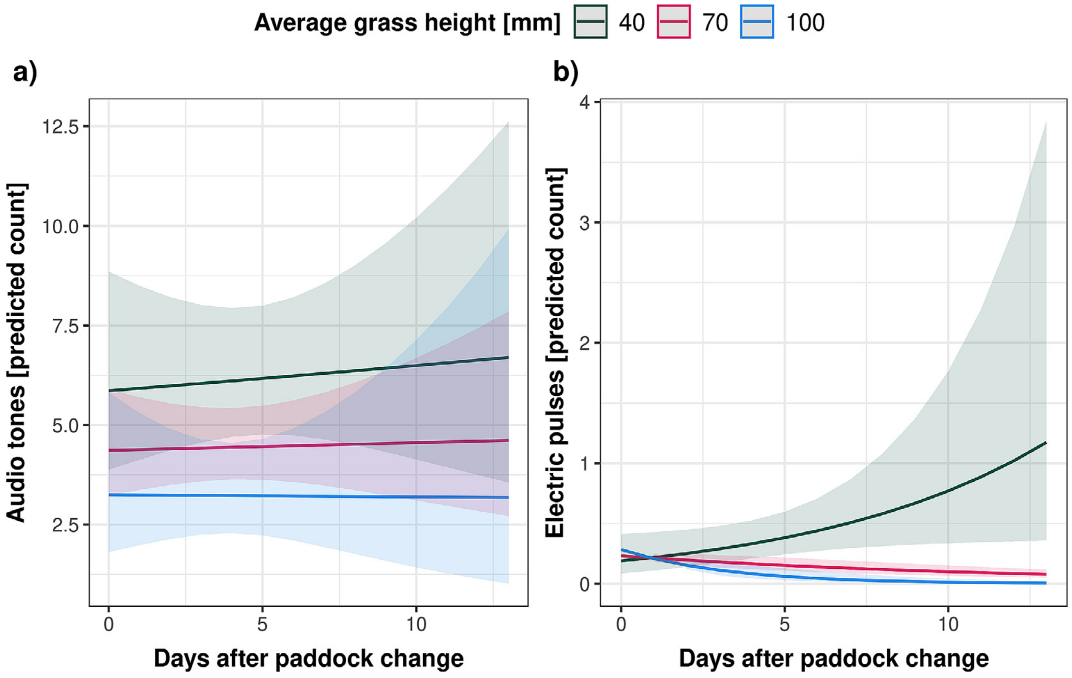

**Fig. 3.** Plots showing the predicted mean number (solid lines) of (a) audio tones and (b) electric pulses within their confidence intervals (color shading), depending on the interaction between days after paddock change and average grass height during the heifer's mountain grazing.

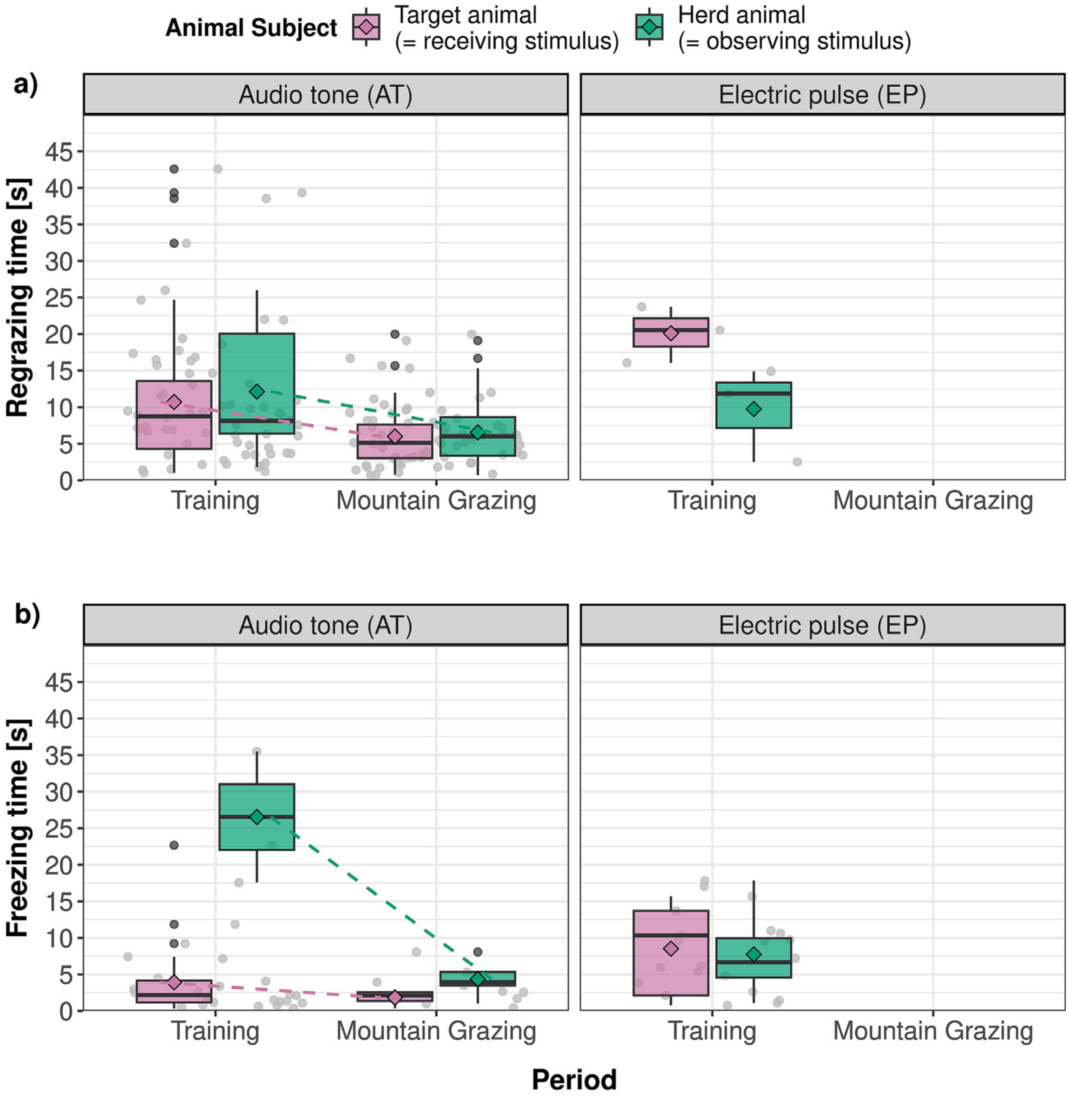

**Fig. 4.** Duration of (a) regrazing time (start grazing again) and (b) freezing time (staring without any movement) after target animals (in pink) were exposed to a stimulus or herd animals (in green) observed one during the two experimental stages (training and mountain grazing). A target animal was defined as a heifer that was exposed to an audio tone (AT) or electric pulse (EP). A herd animal was defined as a single heifer from the herd that observed a target animal receiving a stimulus (e.g., head and ear position directed towards the target animal), but did not experience the stimulus itself. The mean duration is indicated by the square, and the median duration is indicated by the black solid line within each boxplot. The scattered light grey dots represent individual observations, and the dark grey dots represent data outliers. The generalised regression is shown along the dashed line. In response to an EP during mountain grazing, regrazing and freezing were never documented, hence the missing box plots.

successful learning in beef (Verdon et al., 2021a; Aaser et al., 2022; Hamidi et al., 2024) and dairy cattle (Lomax et al., 2019; Fuchs et al., 2024).

Moreover, the mean success ratio more than doubled after three training days, showing that the learning progress was greatest during the first 72 -h. This finding aligns with previous research demonstrating peak learning in cattle within the first two (Campbell et al., 2018; Confessore et al., 2024), 3 (Fuchs et al., 2024) and 4 days (Lomax et al., 2019) after initial virtual fence activation. It should be noted that the success ratio is based on the animal's correct response to ATs relative to the number of virtual fence contacts and therefore does not reflect the total amount of VF interactions. Consequently, the success ratio may be 100% for an animal receiving either one or 100 ATs without a subsequent EP, and infrequent interactions could be interpreted as avoidance behaviour rather than successful learning (Hamidi et al., 2024). In the present study, a major decrease in the frequency of VF interactions (e.g., training Day 6) was followed by an increase in the number of ATs and EPs back to a higher level in the following days, indicating that the heifers were not afraid to approach the virtual boundary.

During VF training, we measured fluctuations in the progression of ATs and EPs as well as in the success ratio. The daily variations may be related to the training steps, which required the heifers to adapt to a number of different scenarios at the virtual boundaries. Many of these were novel experiences for the heifers, especially during training period 1. During mountain grazing, the animals had to adapt repeatedly to a different paddock with a new virtual boundary, as well as to a change in their experimental treatment (from EF-only to VF treatment or vice versa). They also had to cope with the more complex environmental conditions of mountain grazing (larger and more heterogeneous paddocks) compared to the training period (smaller and flatter paddocks). Along with the changes in the experimental setup, the heifers thus had to test

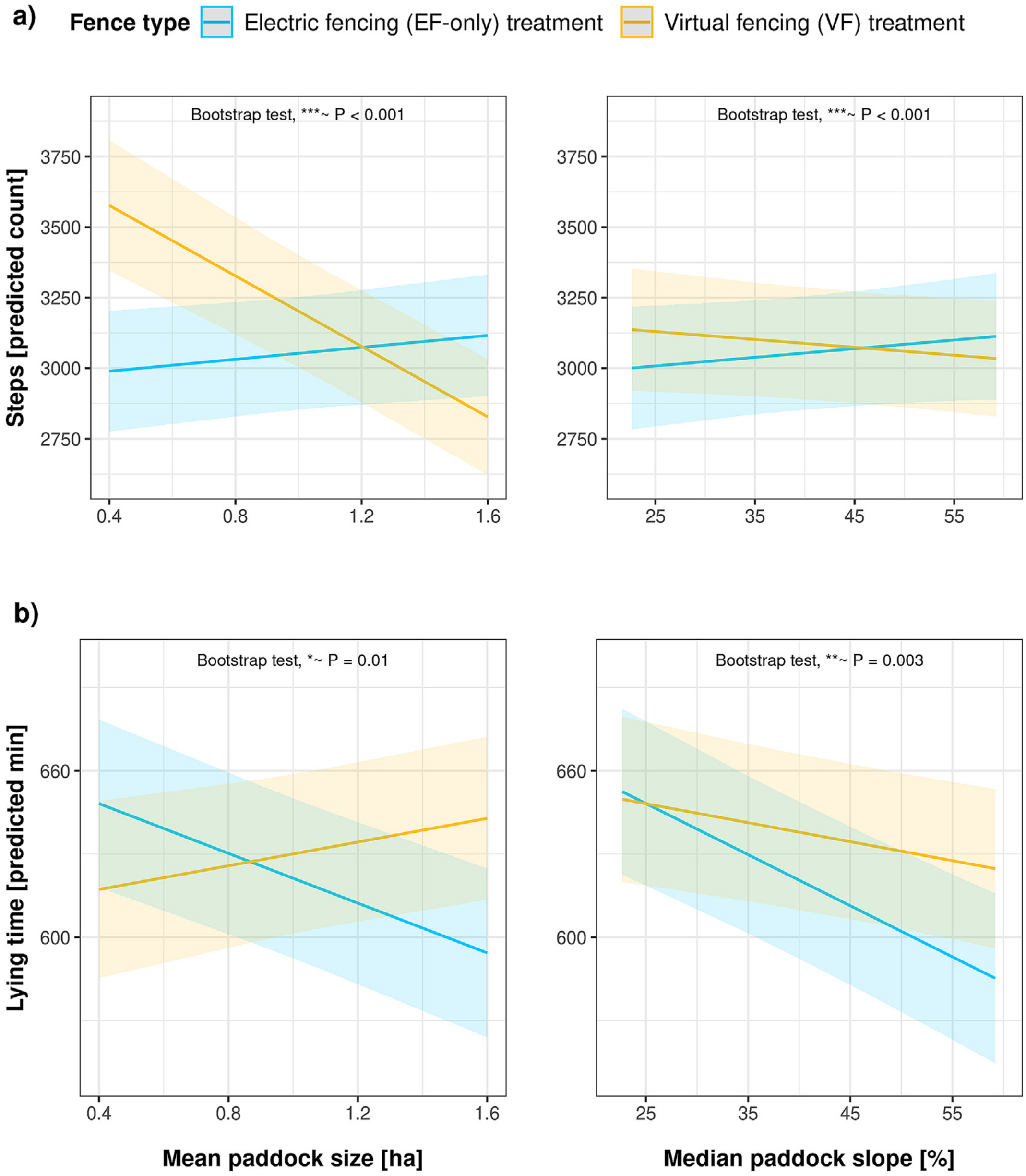

**Fig. 5.** Plots showing the predicted means (solid lines) within their confidence intervals (color shading) for (a) the number of steps and (b) the lying time of the heifers as a function of the interaction of mean paddock size, mean paddock slope and fence type during mountain grazing. Significance levels indicated by $P < 0.001$ (***), $P < 0.01$ (**), $P \leq 0.05$ (*).

the boundaries of their grazing area more frequently to gain a deeper understanding of their territorial limits, especially when switching from EF-only to VF treatment.

Feed shortage may impact cattle behaviour (Schütz et al., 2006; Greter et al., 2015). The results of the present study demonstrate that heifers tested the virtual boundaries more frequently at pasture depletion, indicating a clear motivation to access adjacent areas with fresh grass. As a result, we recorded a higher number of ATs and EPs as grass height decreased. Prior research has demonstrated comparable outcomes, particularly in heifers that tested (Hamidi et al., 2022) and in lactating dairy cows that crossed (Colusso et al., 2021; Langworthy et al., 2021) the virtual boundaries in response to reduced forage availability. Despite the more difficult management and environmental conditions compared to the training period, the success ratio remained at a high mean level (90.9 ± 22.7%) during mountain grazing. This outcome is comparable to that reported by Hamidi et al. (2024) in a lowland environment (91.3%).

Furthermore, the VF system was as reliable as electric fencing in preventing escape events and escaped animals (VF: 17 escaped animals in 8 events; EF: 36 escaped animals in 11 events), as confirmed by Fisher's exact test. However, it needs to be considered that there were more replicates for EF escapes (three groups) than for VF escapes (two groups). From a practical point of view, the rate of escape events is particularly important relative to the number of animals involved per event. In VF, each animal is confined by an individual virtual boundary rather than a shared physical barrier. Consequently, the escape of an individual does not compromise the physical containment of others (Waterhouse, 2023). Escaped individuals in VF systems typically return to their group on their own, as documented by Wallington (2021) and also observed in the present study. The VF design allows animals to re-enter their grazing area without deterrence. In contrast, EF escapes are often caused by one or two animals damaging the physical barrier, or especially in mountainous areas, also by wildlife crossings. Damage to the physical barrier can cause entire sections of the fence to

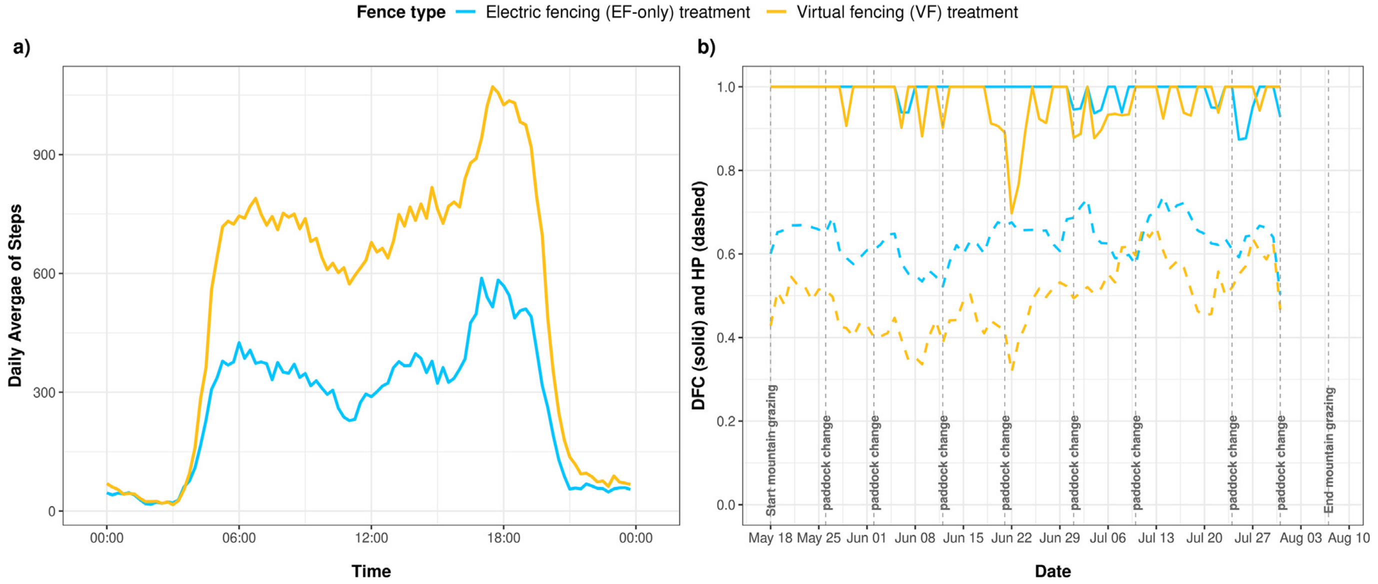

**Fig. 6.** Graphs showing (a) the average daily step count and (b) the Degree of Functional Coupling (DFC) and Harmonic Part (HP) measured in the heifers during mountain grazing according to fence type. The DFC is shown as solid lines, and the HP is shown as dashed lines for both fence types. The average daily step count was calculated by taking one data point per heifer per day at the specified time and averaging all values across all days of mountain grazing. The DFC and HP were calculated based on a step count interval of 15 min over a sliding 7-day period throughout mountain grazing.

collapse, triggering the escape of groups of animals (Waterhouse, 2023). Also in our study, EF escapes involved a higher number of animals escaping from their designated paddock. The EF escapes require additional work to repair the fence and herd back the escaped animals, risking injury and stress to both animals and staff (Waterhouse, 2023). In addition, EF systems lack real-time monitoring, resulting in delayed detection of escapes and the risk of extended unauthorised animal access to restricted areas.

### *Unforeseen events increased the number of audio tones, electric pulses and escapes*

During 81 days of mountain grazing, we documented a total of 15 unforeseen events that occurred on 13 different days. These included the presence of neighbouring cattle, wildlife encounters, a mobile network outage, and damage to electric fences. Such events are likely to occur in mountainous regions and are of importance with regard to animal welfare. Our study demonstrated a significant increase in the number of both ATs and EPs on days with unforeseen events compared to days without such occurrences. In addition, we documented escapes from both VF and EF, which can be attributed in part to certain unforeseen events.

In particular, the presence of neighbouring cattle represented a strong attractant for the animals, as also reported by Verdon et al. (2021a). During mountain grazing, we observed heifers trying to approach neighbouring cattle by crossing the virtual fence. Similarly, neighbouring cattle tried to interact with the heifers, even breaking through the electric fence of their paddock and entering the virtually fenced area of our heifers. Thus, there is a certain power of attraction between conspecifics in sight which can lead to a reduction in virtual fence- and also electric fence efficacy.

### *Heifers were able to cope with virtual fencing in mountainous terrain*

Irrespective of the challenging conditions presented by mountainous terrain and various external factors influencing animal behaviour, the heifers adapted to the VF system. Our results demonstrate that the heifers responded to ATs mostly by turning back at the virtual fences into their designated grazing area, thereby preventing a potential EP. This was reflected in a success ratio of 90.9 ± 22.7% during mountain grazing. The finding is in line with the responses previously observed in sheep (Marini et al., 2018a; Marini et al., 2018b), beef (Lee et al., 2009; Hamidi et al., 2024) and dairy cattle (Colusso et al., 2020; Verdon et al., 2021b; Fuchs et al., 2024). Moreover, our results indicate that the animals reacted increasingly appropriately to the VF stimuli as learning progressed. The frequency of turning around and walking away from the boundary (retreat) in response to an EP increased from training to mountain grazing, whereas the frequency of turning around and running in such situations decreased.

Also, as a result of animal learning, the duration of grazing interruptions (e.g., time before regrazing and freezing time) in response to an AT decreased from VF training to mountain grazing for both target and herd animals. Furthermore, our findings revealed longer grazing interruptions in response to an EP compared to an AT, with particularly longer intervals for target than herd animals. During VF training, target animals took about twice the time to start grazing again when exposed to an EP compared to ATs. Consequently, EPs had a more disruptive effect than ATs, and particularly on target animals that were exposed to the stimuli. This was also reflected in the frequency of running, which was higher in response to an EP than an AT. Interestingly, grazing interruptions in response to an AT were longer in herd compared to target animals. This finding may be explained by the fact that target animals need to respond promptly at the virtual boundary in order to avoid an EP. In contrast, herd animals may benefit from observing the potential implications at the virtual boundary. This conclusion is supported by previous findings, documenting a collaborative learning in cattle by observing the reactions of conspecifics at the virtual boundary (Colusso et al., 2020; Keshavarzi et al., 2020; Aaser et al., 2022).

### *Activity behaviour was influenced by paddock characteristics*

The daily number of steps taken by the heifers was not affected by VF use. However, lying time was about 10 min per day longer when heifers grazed in the VF treatment compared to the EF-only treatment. This finding is contrary to the results of Campbell et al. (2019), who found shorter lying time in virtually fenced cattle groups compared to electrically fenced groups. Even though the time discrepancies were statistically significant, they represent a negligible difference over the course of a day from a biological perspective, as well as taking into account intra-individual (Ito et al., 2009) and inter-individual (Arnold, 1984) variations in total lying time among cattle. Accordingly, it can be assumed that the slight difference in the duration of lying time between VF and EF-only treatments provided no indication of a meaningful impact upon animal time budgets or well-being. Additionally, our findings indicate that the interaction between fence type and mean paddock size or median paddock slope had a significant impact on step count and lying time. These results may be linked to the natural variability of environmental conditions in the present study, which differ from those typically found in controlled research settings. Paddock sizes in the present study varied according to expected forage yield to ensure comparable grazing duration across paddocks. In addition, EF-only paddocks and VF paddocks differed in median slope, although comparability between fence types was sought but not always achieved due to the complexity of the experimental design and management practices in mountain areas. As a result, paddock characteristics varied both between and within fence types, with statistically significant but biologically meaningless effects on activity behaviour.

### *Circadian activity rhythmicity was not affected by fence type*

Heifers exhibited a diurnal activity rhythm with increased activity levels in the early morning and late afternoon hours, which is representative of beef cattle grazing on alpine summer pastures (Probo et al., 2014). In addition, activity patterns were highly rhythmic, as indicated by mean DFC values greater than 0.92, regardless of fence type. This finding may be related to the extensive livestock system, as previous research has revealed high DFC levels in particularly extensively managed species such as sheep (Scheibe et al., 1999; Nunes Marsiglio Sarout et al., 2018), alpaca, deer, and mouflon (Scheibe et al., 1999; Berger et al., 2002; Berger et al., 2003; Berger, 2011), as well as wild horses (resp. Przewalski) (Scheibe et al., 1999; Berger et al., 2003; Berger, 2011). Moreover, circadian activity rhythms have also been identified in housed lactating dairy cows (Fuchs et al., 2022). In combination, these studies have shown that the DFC reaches high values in well-adapted and healthy animals, but decreases during periods of calving, medical treatment, or adaptation (e.g., seasonal variation, hunting, social stress, disease, transportation). The present study found that relocating heifers to a new paddock within the VF treatment resulted in a decrease in DFC values. Conversely, there was no impact of paddock changes within the EF-only treatments. As shown in Fig. 6, the decline in DFC within the VF treatments was most evident following the fourth paddock change during mountain grazing. When examining the trend of DFC for each group separately, we found that the sharp decrease in DFC after the fourth paddock change could mainly be related to group A. However, the reason for this result is unclear. For the remaining grazing period, the overall DFC increased again and remained at higher levels, despite the repeated relocation of the heifers to new paddocks.

## Conclusions

The heifers were able to adapt to the VF technology even under challenging mountain conditions. The animals reacted appropriately to ATs, thus learning to avoid EPs, and grazing interruptions upon virtual fence contact became shorter over time. The activity behaviour was comparable between EF-only and VF treatments. Rhythmic circadian activity, reflected by a high DFC, supported the hypothesis that long-term animal welfare was not compromised by VF use. Throughout mountain grazing, the VF system was equally reliable as electric fencing in preventing escapes. Therefore, the VF technology could be a beneficial tool for mountain livestock grazing, facilitating fencing work and offering the advantages of remote animal monitoring.

## Supplementary material

Supplementary Material for this article (https://doi.org/10.1016/j.animal.2025.101600) can be found at the foot of the online page, in the Appendix section.

## Ethics approval

All experimental procedures were approved by the Cantonal Veterinary Office of the Canton of Vaud, according to the Swiss Animal Protection Ordinance (authorisation number N35488-2023-VD).

## Data and model availability statement

None of the data were deposited in an official repository but data and models are available upon request.

## Declaration of Generative AI and AI-assisted technologies in the writing process

During the preparation of this work the author(s) did not use any AI and AI-assisted technologies.

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## Declaration of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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