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Behavioral responses of blue sheep (*Pseudois nayaur*) to nonlethal human recreational disturbance

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Nonlethal human recreational activities have been confirmed to have negative effect on wild animals in a number of ways, including changes in behaviors, avoidance of suitable habitats and declines in breeding success. Studies on the anti-disturbance mechanism of wild animals to human disturbance can provide valuable knowledge to the management of wild animals and the evolutionary mechanisms of behavioral adaptation to their habitats. To evaluate how blue sheep (*Pseudois nayaur*) would react to nonlethal human recreational disturbance, we studied their anti-disturbance strategy towards human disturbance in Suyukou National Forest Park (SNFP), Helan Mountains, Yinchuan of Ningxia Hui Autonomous Region. Using multinomial logistic regression models (MLRMs), we sought to answer two questions: (1) which kind of human recreational behavior would evoke the most serious anti-disturbance behaviors in blue sheep; and (2) how would various ecological factors influence the anti-disturbance strategy of blue sheep to human recreational disturbance? We collected 10 habitat and population variables and evaluated three kinds of reaction of blue sheep–no response, vigilance and flight. A total of 921 observations qualified to enter MLRMs. We found that habitat type (HT), gender (GEN), head direction (HD), visibility index (VI), and disturbance source (DS) were the five variables that significantly influenced the intensity of reactions of blue sheep. Blue sheep were more alert to tourists than to vehicles, and roads were the habitat type that caused the most intensive reaction of alertness where human disturbance was the highest. Females were more vigilant than males. Blue sheep might feel safer when staying in open habitat, and taking a front head direction provided them with the highest vigilance. Based on these results, we present suggestions to SNFP for the management of ecotourism and blue sheep conservation.

recreational disturbance, blue sheep, multinomial logistic regression models, alertness

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Predator-prey interaction is one of the key topics of behavior ecology research because predation significantly impacts on prey population dynamics, prey behavior and ecosystem function as a whole [1]. Recently, nonlethal human-related recreational activities such as ecotourism have been increasing rapidly. This novel and important threat evokes reactions in wildlife that resemble anti-predator responses [2,3]. However, this kind of threat is vastly different from the traditional predation risk in terms of types, degree of effects and interactions with circumstances [4]. Some studies have found that human disturbance leads to changes in responses of animals to risk and other alterations in ecological processes, such as decline in fitness, changes in interspecific interactions, increased energetic costs, avoidance of other suitable habitats, and changes in species communities [4–7]. Vigilance (or alert) and flight (or flush) are two im-

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portant anti-predator behaviors. However, when any type of risky stimuli in context exceeds a certain threshold, wild animals would generally make reactions analogous to anti-predator responses to threats of the same level [3,8]. Therefore, studies on the anti-disturbance mechanisms of wild animals to human disturbance can provide valuable knowledge for the management of wild animals and expand our understanding of the evolutionary mechanisms behind behavioral adaptation to disturbed habitats.

Blue sheep (*Pseudois nayaur*) have been listed as second grade nationally protected animals in China. The Helan Mountains National Nature Reserve (HMNNR) was established in 1988 in the Helan Mountains in Ningxia Hui Autonomous Region, and is one of the main habitat sites for blue sheep. The latest survey indicated that approximately 10000 blue sheep were distributed in the nature reserve [9]. Because mining, poaching, and pasturing are currently prohibited throughout the nature reserve, ecotourism is the primary human activity and source of disturbance (HMNNR unpublished data, 2006). To facilitate this tourism, roads have been built alongside mountains that cross habitats of blue sheep. Nevertheless, the negative influence of ecotourism to the survival of blue sheep has never been empirically evaluated.

Three kinds of anti-disturbance reactions of wild animals—no response, vigilance, and flight—usually indicate the stimulus is increasing in intensity. Consequently, these reaction behaviors are frequently used to assess the degree of vulnerability of wild animals toward a stimulus [10]. In addition to the features of the stimulus [11,12], wild animals would integrate various factors into their decision-making of anti-predator strategy, such as the group size, gender and distance to cover [13–15]. By taking all such factors into account, wild animals follow an economic model to balance the costs of avoiding disturbance and remaining in their habitat [16–18]. Consequently, we tried to answer two questions in this paper: (1) which kind of human recreational behavior would evoke the most serious anti-disturbance behaviors in blue sheep; and (2) how would various ecological factors influence the anti-disturbance strategy of blue sheep to human recreational disturbance?

1 Materials and methods

1.1 Study area

We conducted this study in the Suyukou National Forest Park (SNFP), which is located in the eastern part of HMNNR (38°42′N–38°46′N, 103°42′E–106°E) covering a 96 km^2 area with elevation ranging from 1000–2800 m. The climate in SNFP is cool and dry. The mean highest month temperature was 22.3°C in July and the lowest was −13.2°C in January, and the annual precipitation was 131 mm with only about 37 mm rainfall during the study period (HMNNR unpublished data, 2010).

The main land cover forms in the study area are the mountain open forest and the mountain steppe. *Ulmus glaucescens* and *Populus davidiara* are the main tree species, and the main shrub species include *Prunus mongolica*, *Dasiphora* spp., and *Caragana stenophylla* [19]. Blue sheep, red deer (*Cervus elaphus*), and alpine musk deer (*Moschus chrysogaster*) are the only three large herbivores recorded in this region. Predators (i.e. the snow leopard *Uncia uncia*, wolf *Canis lupus* and the Eurasian lynx *Lynx lynx*) of large herbivores have not been observed since the 1980s [20].

Suyukou National Forest Park was opened to the public as a tourism site in the 1980s. Hunting has been forbidden in this area since 1988, all mining sites in the forest park were closed in 2001, and farmers in the neighborhood moved out of the park in 2004. As a consequence, tourism is the main source of human disturbance in the study area. The forest park attracts more than 100000 visitors annually (SNFP unpublished data, 2005 to 2010). Summer (June–August) is the peak season with a mean number of 32284 visitors (29537 in the summer of 2007, 29926 in 2008, 38073 in 2009, 31598 in 2010). Tourists and vehicles are the two main types of human disturbance in the forest park. Vehicles drive on the paved road, while tourists may disembark from the vehicle and walk along the road.

1.2 Field observation

All observations were made along fixed transects in July and August 2010. Transects were designed to cover all the routes that tourists visit in the study area. In total, four transects were surveyed with a total length of 18.3 km including 9.8 km of the main paved road of the park, 3.5 km of the Lingxiang Road, 3 km of the Cherry valley, and 2 km of the Wang ravine. Surveys were conducted during the day, from 06:00 am to 11:00 am and from 16:00 pm to 19:30 pm, covering the two activity peaks of blue sheep [21]. Two observers evaluated the reactions of blue sheep to the disturbance source in a range of 500 m on both sides of the transect.

To simulate and evaluate disturbance from tourists, observers walked normally on transects at a speed of 2 km/h. For evaluation of vehicle disturbance, observers watched blue sheep from a sightseeing bus that was driving on the road. Reactions of blue sheep were observed using 10×42 mm binoculars, and their reactions to human disturbance were recorded. Blue sheep can be found solitarily or in groups [16]. When in groups, we recorded the behavior of the first individual reacting to the disturbance. We classified the reaction of blue sheep into three kinds: (1) no response (N): no individual noticed the disturbance or they noticed but resumed the prior act; (2) vigilance (V): the subject individual lifted its head and kept vigilant until the observer left; and (3) flight (F): the subject individual moved away.

Variables needed for the construction of the multinomial logistic regression model were evaluated and recorded for each observed interaction of blue sheep and human disturbance (see below).

1.3 Variables for multinomial logistic regression models

To evaluate the reaction of blue sheep towards human disturbance, we established multinomial logistic regression models (MLRMs) [22]. Data of 10 environmental and populational variables were collected.

(1) Disturbance source (DS). Tourists and vehicles are the two main sources of human disturbance in the forest park. In this study, as described above, tourist disturbance was simulated by two walking observers and vehicle disturbance was evaluated by observation from SNFP sightseeing buses. We quantified the tourists as one, and the vehicle as two (tourists=1, vehicle=2).

(2) Reaction distance (RD). The distance between the reacting animal and the provoking disturbance source [23]. Sometimes, especially when blue sheep stayed near roads, they displayed their whole behavior spectrum from no response to flight when the observer was moving on the road. In this case, the reaction distance of the response was determined by the distance at which each kind of the three responses (i.e. N, V, and F responses) was initiated. We named these distances as the no response distance (N distance), the vigilance initiation distance (V distance), and the flight initiation distance (F distance).

(3) Perpendicular distance (PD). The shortest straight-line distance between the transect and the initial position where the animal was observed initiating its response to the disturbance [14]. Distance data of RD and PD were measured by a Bushnell Yardage pro 800 rangefinder (Bushnell, Overland Park, Kansas, USA).

(4) Vertical angle (VA). To investigate whether the upper or lower position of blue sheep relative to the observer would influence their reaction, we measured the vertical angle between the objective and the observer. The vertical angle was zero when the observer and the blue sheep were at the same horizontal level. Negative vertical angles could be measured when the blue sheep was located lower than the observer. Positive angles were recorded when the blue sheep was located higher than the observer.

(5) Head direction (HD). Head direction is categorized into three types—front, side, and back. To quantify head directions, we set back=1, side=2, front=3. Front denotes the face of the animal, which is frontal to the observer prior to its reaction. Side denotes the observer watching the subject animal from the side. Back indicates the observer watching the animal from the rear or the animal is invisible to the observer. We excluded the observation when the head of the animal was hidden behind obstacles.

(6) Group size (GS). Number of individuals in the group to which the subject blue sheep belonged. If a single blue sheep was observed, the group size was always one.

(7) Group type (GT). We defined four types—single (only one individual, female or male adult), female group (adult females with yearlings or juveniles. We did not observe groups with only adult females), male group (adult males only), mixed group with at least one adult female and adult male [24]. We set the single=1, female group=2, male group=3, and mixed group=4.

(8) Gender (GEN). We set the adult male=1, and the adult female=2. Gender of the blue sheep can be distinguished in the field by the individual's horns. The horns of adult females are smaller, thinner and more upright with no inward curl, compared with those of adult males [25]. When a single individual was observed, its gender was distinguished and recorded. When grouped blue sheep, especially in a mixed group, were observed, we distinguished and recorded the gender of the first individual in the group that reacted to human disturbance.

(9) Visibility index (VI). Since shrubs and rocks usually covered the animal at the initial position, we calculated a blue sheep's visibility index by using the proportion of the visible part of its body.

(10) Habitat type (HT). We defined three kinds of habitat—road (covering the paved road and flat area with a 50 m width of each roadside), cliff (located on rocky mountains with slopes above 10°), and ravine (the flat area remaining, excluding road and cliff). We set ravine=1, cliff=2, and road=3.

1.4 Multinomial logistic regression model

Multinomial logistic regression models (MLRMs) were used to fit the blue sheep reaction to human disturbance because there were three response categories (N, V, and F) [22,26]. Two logits were modeled:

$$LogitP_1 = \ln\left[\frac{P_1(X)}{P_0(X)}\right]$$

and

$$LogitP_2 = \ln\left[\frac{P_2(X)}{P_0(X)}\right],$$

where P_0(X), P_1(X), and P_2(X) are, respectively, the probabilities of an N response, V response, and F response given $X=(x_1, x_2, x_3, \cdots x_n|n\leqslant 10)$ is a covariate vector of models (i.e. the ten variables explained above). We treated no response (N response) as the baseline response by using P_0(X) to be in the denominator of each logit (odds). To calculate MLRMs, all the variables involved should be independent from each other [27]. We judged Spearman correlations between variables, $\rho<0.6$, or (and) the significance value $P>0.05$ as criteria of independence. Pairs of variables with significant correlations could not enter logistic regression at the same time. Coefficients of determination of models were calculated using Nagelkerke pseudo R^2. The second order Akaike index criterion (AIC_c) was given to each model generated. The one with the lowest AIC_c was chosen. However, if the difference of AIC_c values among models were smaller than two, the simplest model was chosen (i.e. the parsimony criterion) [28].

For the chosen model, we wanted to know how a single valid variable would influence the response of animals to human disturbance, therefore two odds ratios were calculated: the odds ratio of vigilance (V) relative to no response (N) (OR_1)

$$OR_1\left(X_i, X_j\right)=\frac{\left[\dfrac{P_1(X_i)}{P_0(X_i)}\right]}{\left[\dfrac{P_1(X_j)}{P_0(X_j)}\right]}$$

and the flight (F) relative to no response (N) (OR_2)

$$OR_2\left(X_i, X_j\right)=\frac{\left[\dfrac{P_2(X_i)}{P_0(X_i)}\right]}{\left[\dfrac{P_2(X_j)}{P_0(X_j)}\right]}.$$

For each quantitative variable (e.g. visibility index, VI), X_i and X_j were selected to calculate the odds ratio for a one unit of measurement increase. For each categorical variable (e.g. the habitat type, HT), X_i was the covariate vector when the *i*th category of this variable was chosen, and X_j was the baseline of this variable (e.g. "road" in the habitat type variable). Since the largest number of categories in a categorical variable in this study is three, *i* and *j* should be ⩽3.

1.5 Statistics

Data in each of the 10 variables were divided into a tourist group and a vehicle group according to the disturbance sources (DS). For the categorical variable, we ran a χ^2 independence test to evaluate whether the incidence of the three kinds of animal reaction was significantly different within the same group. Meanwhile, Wilcoxon signed-rank tests for paired samples were used to analyze the difference in animal reaction between the two groups of the variable. For the numerical variable, we ran a Kruskal-Wallis rank sum test to evaluate the distribution of data in different animal responses in the same group. A paired sample *t* test or a Wilcoxon signed-rank test for paired samples was then used to analyze the difference in animal responses between the two groups of the variable according to whether the data fitted criteria of parametric statistics.

Since response distance is a useful tool to analyze reactions of animals to disturbance [29], we compared the difference of the V distance and F distance among categories of each variable entering the final MLRM. The Kruskal-Wallis test and the Wilcoxon test were used depending on the number of categories compared. For the variable VI, we used a Spearman correlation analysis to test the relationship between VI and response distance.

To avoid the problem of inequality of data size between the two compared data groups [30], the group with larger data size would first be bootstrap resampled with a size equal to the variable with the smaller data size, then the *t*, Wilcoxon, and Kruskal-Wallis tests would be conducted. For each test, the bootstrap was repeated 100 times. All the statistical works and MLRMs modeling were conducted using R 2.13.2 (http://www.r-project.org/).

2 Results

We had a total of 921 observations qualified to enter MLRMs, 139 observations in vehicle and 782 as tourists. Results of the statistical analysis of the 10 variables are listed in Table 1. Data in the reaction distance (RD) and the perpendicular distance (PD) both revealed significant differences in the reaction distance of blue sheep with the largest mean N distance, the shortest mean F distance, and with mean V distance in the middle, regardless of whether it was the tourist or vehicle group (Table 1). Data in RD further revealed that reaction distances in the tourist group were significantly larger than those in the vehicle group (t_2=11.1, P=0.008, Table 1). The head direction (HD) significantly influenced the vigilance response both in the tourist (χ^2_4=202.491, P<0.001) and vehicle (χ^2_4=27.146, P<0.001) groups. Kruskal-Wallis rank sum tests found that both the group type (GT) and gender (GEN) significantly influenced responses of blue sheep to tourist disturbance, but not to vehicle disturbance (Table 1). Habitat type (HT) also significantly influenced the reaction of blue sheep both in the tourist (χ^2_4= 115.641, P<0.001) and vehicle (χ^2_4=56.351, P<0.001) groups of the three kinds of responses (Table 1). However, data in vertical angle (VA), group size (GS), and visibility index (VI) did not significantly influence responses of blue sheep either in the tourist or vehicle groups (Table 1).

2.1 MLRM formulation

Four pairs of variables, RD–PD, GS–GT, HT–PD, and HT–VA were found to be significantly correlated (Table 2). Therefore, the two variables in each pair were not inputted into the same logistic regression model. Thus, we developed nine candidate MLRMs (Table 3). Among these models, the model nine had the smallest AICc value, and was therefore selected as the final model (Table 3). Among the five valid variables in the final model, HD and HT are ternary variables, DS and GEN are binary variables, and VI is a quantitative variable. When developing a MLRM, reference category to each categorical variable must be set in advance. We set "road" as the referential category in HT, "back" in HD, "vehicle" in DS, and "female" in GEN. Odds ratios for

Table 1 Data statistics of the 10 ecological variables for the behavioral response evaluation of blue sheep in the Suyukou National Forest Park (SNFP)

Variables	Disturbance source	Data	Alert behavior (number of observations)			Statistics	
			N	V	F	Within the same DS	Between the two kinds of DS[a)]
Disturbance source (DS)	Tourist		198	204	380		
	Vehicle		116	6	17		
Reaction distance (RD) (m)	Tourist	70.5±37.8 (6–215)	198			χ_2^2=123.187***	*t*=11.1**
		48.1±23.9 (6–156)		204			
		39.0±21.5 (4–109)			380		
	Vehicle	46.8±25.1 (6–150)	115			χ_2^2= 22.019***	
		30.8±18.1 (6–52)		6			
		17.8±17.5 (3–52)			17		
Perpendicular distance (PD) (m)	Tourist	57.0±40.6 (0–200)	181			χ_2^2=204.002***	*t*=1.312
		28.2±23.6 (0–120)		180			*P*=0.320
		14.8±17.4 (0–100)			357		
	Vehicle	34.4±26.9 (6–150)	111			χ_2^2= 16.528***	
		27.2±18.3 (6–53)		6			
		11.4±18.7 (3–50)			16		
Vertical angle (VA) (°)	Tourist	1.4±12.8 (–25–50)	198			χ_2^2=4.790	*t*=3.618
		4.9±17.0 (–40–45)		204		*P*=0.091	*P*=0.069
		1.0±12.1 (–35–45)			380		
	Vehicle	–3.4±14.8 (–27–50)	116			χ_2^2=1.599	
		–2.5±4.2 (–10–0)		6		*P*=0.408	
		–1.7±12.7 (–20–40)			17		
Head direction (HD)	Tourist	Front	44	5	280	χ_4^2=202.491***	
		Side	138	125	280		
		Back	8	58	38		
	Vehicle	Front	13	0	15	χ_4^2=27.146***	
		Side	82	5	15		
		Back	17	0	0		
Group size (GS)	Tourist	3.3±2.2 (1–14)	198			χ_2^2=9.397**	*t*=0.509
		3.7±3.1 (1–26)		204			*P*=0.661
		3.0±2.2 (1–15)			379		
	Vehicle	3.5±2.4 (1–15)	115			χ_4^2=1.909	
		2.5±2.0 (1–5)		6		*P*=0.385	
		3.3±2.9 (1–11)			17		
Group type (GT)	Tourist	Single	38	36	101	χ_6^2=15.062*	
		Female	103	93	190		
		Male	13	17	24		
		Mixed	36	42	45		
	Vehicle	Single	22	3	3	χ_6^2=5.202	
		Female	67	2	10	*P*=0.518	
		Male	6	0	1		
		Mixed	17	0	2		
Gender (GEN)	Tourist	Male	62	71	85	χ_2^2=12.971**	
		Female	130	118	277		
	Vehicle	Male	23	1	5	χ_2^2=0.953	
		Female	89	4	11	*P*=0.621	
Visibility index (VI)	Tourist	0.88±0.23 (0–1)	198			χ_2^2=5.143	*t*=2.320
		0.82±0.25 (0.01–1)		204		*P*=0.076	*P*=0.146
		0.82±0.29 (0.03–1)			380		
	Vehicle	0.90±0.19 (0.27–1)	116			χ_2^2=4.135	
		0.95±0.11 (0.72–1)		6		*P*=0.127	
		0.98±0.06 (0.76–1)			17		
Habitat type (HT)	Tourist	Ravine	121	104	157	χ_4^2=115.641***	
		Cliff	70	84	89		
		Road	4	16	131		
	Vehicle	Ravine	85	5	5	χ_4^2=56.351***	
		Cliff	27	0	1		
		Road	4	1	11		

a) Data in the tourist group were compared with that in the vehicle group in each variable. * $P\leqslant 0.05$; ** $P\leqslant 0.01$; *** $P\leqslant 0.001$.

Table 2 Spearman correlation of the ten variables for the behavioral response evaluation of blue sheep[a)]

	DS	RD	PD	VA	HD	GS	GT	GEN	VI	HT
DS	–									
RD	–0.073*	–								
PD	0.077*	0.655**	–							
VA	–0.168**	–0.065*	–0.313**	–						
HD	–0.003	–0.057	0.002	0.008	–					
GS	0.031	0.154**	0.203**	–0.150**	–0.011	–				
GT	–0.006	0.101**	0.110**	–0.028	–0.023	0.700**	–			
GEN	0.060	0.020	0.025	–0.160**	0.033	0.087**	–0.421**	–		
VI	0.094**	0.122**	0.166**	–0.304**	0.018	0.075*	0.015	0.107**	–	
HT	–0.133**	0.256**	–0.675**	0.571**	0.040	–0.159**	–0.044	–0.130**	–0.139**	–

a) *$P\leqslant 0.05$, ** $P\leqslant 0.01$. DS, Disturbance source; RD, reaction distance; PD, perpendicular distance; VA, vertical angle; HD, head direction; GS, group size; GT, group type; GEN, gender; VI, visibility index; HT, habitat type. Correlations did not reach the 0.05 level of significance or reached but the correlation value was less than 0.5 were judged as not significant.

Table 3 Comparison of the nine candidate multinomial logistic regression models (MLRMs) for behavioral responses of blue sheep

Number of models	Vector of variables	$R^{2a)}$	AIC_c	ΔAIC_c	W_i
1	DS**, HD**, GEN*, VI**, RD, VA*, GS	0.448	1427	856	<0.001
2	DS**, HD**, GEN*, VI**, RD, VA*, GT	0.450	1413	842	<0.001
3	DS**, HD**, GEN**, VI, PD**, VA**, GS	0.522	1173	602	<0.001
4	DS**, HD**, GEN**, VI, PD**, VA**, GT	0.523	1126	555	<0.001
5	DS**, HD**, GEN**, VI**, HT**, GS	0.449	902	331	<0.001
6	DS**, HD**, GEN**, VI**, HT**, GT	0.450	692	121	<0.001
7	DS**, RD**, HD**, GEN**, VA*	0.450	1303	732	<0.001
8	DS**, PD**, HD**, GEN**, VA**	0.520	943	372	<0.001
9	DS**, HT**, HD**, GEN**, VI**	0.450	571	0	1.000

a) Nagelkerke R^2. *, ** denoted significant variables at 0.05 and 0.01 level respectively. DS, Disturbance source; PD, perpendicular distance; HD, head direction; GEN, gender; HT, habitat type; GT, group type; GS, group size; RD, reaction distance; VA, vertical angle; VI, visibility index. W_i Akaike weight of each model, W_i=exp (–0.5 ΔAIC_c)/Σexp (–0.5 ΔAIC_c).

all five variables in different status were calculated (Tables 4 and 5).

2.2 Model behavior

(1) Vigilance versus no response. We found that the odds ratio of the V relative to N response decreased significantly when the habitat type (HT) changed from road to ravine (*B*=−1.894, *P*<0.001), and from road to cliff (*B*= −1.735, *P*=0.002). Correspondingly, the odds ratio of V to N response reduced to 15.1% (i.e. *OR*=0.151) by staying in the ravine and 17.6% by staying on the cliff (Table 4). The V distances had significant differences among the three kinds of HT with the shortest distance on the road and the largest in the ravine (Table 4). On the contrary, HD had significant influence on the increase of probability of vigilance when blue sheep changed their head direction from back to front (*B*=3.799, *P*<0.001) or side (*B*=2.181, *P*< 0.001). If blue sheep took a front or side position to disturbance, the odds ratio of the V to N response were 44.678 and 8.855 times greater than if they kept their back toward the disturbance (Table 4). However, we did not find a significant difference to the V distance among the three HD categories (χ^2_2=1.476, *P*=0.478, Table 4). For the DS variable, tourists evoked significantly higher incidence of V response compared with the vehicle (*B*=3.438, *OR*=31.13, *P*< 0.001), but the V distance did not differ significantly (*W*=864.5, *P*=0.086, Table 4). GEN did not significantly influence the probability of the V response (*B*=0.113, *P*= 0.624). Similarly, VI of each individual had no significant effect on the probability of vigilance (*B*=–0.790, *P*=0.087), and VI had no significant relationship with the V distance (ρ=0.054, *P*=0.437).

(2) Flight versus no response. The odds ratio of the F response relative to the N response declined significantly when blue sheep changed their location from road to ravine (*B*=–3.767, *P*<0.001) and cliff (*B*=–3.888, *P*<0.001). The odds ratio of the F to N response decreased to 0.02 when

Table 4 Odds ratios of vigilance (V) versus no response (N) in variables in the final MLRM and the comparison of the vigilance initiation distance among categories in each variable[a)]

Variables	Regression coefficient (*B*)	Wald χ^2	*P*	Odds ratio (*OR*)	Vigilance initiation distance (*n*) (m)
Habitat type (HT)^{KW}					
Road^r	3.629				43.7±29.3(17)*
Ravine	−1.894	12.288	<0.001	0.151	50.59±23.8(109)*
Cliff	−1.735	9.820	0.002	0.176	44.7±22.5(84)*
Disturbance source (DS)^W					
Vehicle^r	−3.438				30.8±18.1(6)
Tourist	3.438	49.013	<0.001	31.127	48.2±23.9(204)
Head direction (HD)^{KW}					
Back^r	−5.98				48.5±25.1(58)
Front	3.799	45.889	<0.001	44.678	35.4±15.0(5)
Side	2.181	19.899	<0.001	8.855	46.33±21.4(130)
Gender (GEN)^W					
Female^r	−0.113				48.0±25.0(132)
Male	0.113	0.240	0.624	1.120	47.4±22.0(76)
Visibility index (VI)^S	−0.790	2.927	0.087	0.454	47.7±23.9(210)
B_0	−3.253	12.503	<0.001		

a) * P⩽0.05. r, The referential category. KW, Kruskal-Wallis rank sum test (K-W test) results of the vigilance initiation distance of different varables: HT, χ^2_2=5.889, P=0.050; HD, χ^2_2=1.476, P=0.478, not significant.W, Wilcoxon rank sum test results of the vigilance initiation distance of different varables: DS, W=864.5, P=0.086; GEN, W=5092, P=0.8566. S to VI, a Spearman correlation test was conducted, and no significant correlation was found: ρ=0.054, P= 0.437.

Table 5 Odds ratios of flight (F) versus no response (N) in variables of the final MLRM and the comparison of the flight initiation distance among categories in each variable

Variables	Regression coefficient (*B*)	Wald χ^2	*P*	Odds ratio (*OR*)	Flight initiation distance (*n*) (m)
Habitat type (HT)^{KW}					
Road^r	7.655				31.1±20.7(142)***
Ravine	−3.767	64.310	<0.001	0.023	41.9±20.6(162)***
Cliff	−3.888	63.465	<0.001	0.020	42.9±22.6(90)***
Disturbance source (DS)^W					
Vehicle^r	−3.220				17.8±17.5(17)***
Tourist	3.220	73.901	<0.001	25.039	39.0±21.5(380)***
Head direction (HD)^{KW}					
Back^r	−2.355				40.2±17.3(38)***
Front	1.431	12.298	<0.001	4.181	47.3±23.7(49)***
Side	0.924	11.471	0.001	2.520	39.7±21.5(295)***
Gender (GEN)^W					
Female^r	0.675				39.3±21.6(302)*
Male	−0.675	9.472	0.002	0.509	34.5±21.9(95)*
Visibility index (VI)^S	−1.247	9.205	0.002	0.287	38.1±21.7(397)^S
B_0	1.230	3.788	0.050		

* P⩽0.05, ** P⩽0.01, *** P⩽0.001. r, The referential category. KW, Kruskal-Wallis rank sum test results: HT, χ^2_2=30.127, P<0.001; HD, χ^2_2=14.918, P< 0.001. W, Wilcoxon rank sum test results: DS, W=51675, P<0.001; GEN, W=12216, P=0.029. S to VI, a Spearman correlation test was conducted, and no significant correlation was found: ρ=0.083, P=0.096.

staying in the ravine and on the cliff rather than on the road (HT, Table 5). The F distance significantly differed among the three habitat types with the shortest on the road and the largest on the cliff (χ^2_2=30.127, P<0.001). Tourists had a significantly stronger influence (> 25 times than the vehicle) in evoking the incidence of the F response of blue sheep

(DS, B=3.220, P<0.001, OR=25.039, Table 5). The F distances to tourists were significantly larger than those to vehicles (W=51675, P<0.001). On the contrary, the odds of F response rose when the HD of blue sheep oriented from back to front (B=1.431, P<0.001, OR=4.181) and to the side (B=0.924, P<0.001, OR=2.520) (Table 5), although significant differences in the distance of F response was not found among the three HD categories (χ^2_2=3.717, P=0.1559). Compared with females, males were less inclined to flight (GEN, B=–0.675, OR=0.509, P<0.001, Table 5) and had significantly shorter F distances (W=12216, P=0.029). VI of each individual also had a negative effect on the odds of the F response relative to the N response (B=–1.247, P=0.002, OR=0.287), but we did not find significant correlation between VI and the response distance (ρ=0.083, P=0.096, Table 5).

3 Discussion

Although human recreational activities are usually not direct threats to wild animals, they force animals to devote more time and energy to safety-related behaviors (e.g., vigilance) resembling anti-predator strategies, which come at an expense to foraging, reproduction and resting activities [1]. Thus, the trade-off between safety and obtaining resources can affect the life-history strategies of wild animals [31]. However, recreational activities are essential for humans to appreciate nature and to develop an understanding of wild animals for aesthetic, ethical, and educational purposes. Some examples of introducing human recreational activities to conservation programs of endangered species have already had proven success [3]. However, for species of which we do not have sufficient ecological knowledge, it is important to understand the impact of human recreational disturbance on behavior to ensure successful conservation outcomes [32]. We found that different types of human recreational disturbance, habitat characteristics, and behavior patterns, in particular the social behavior patterns of blue sheep, can significantly influence the anti-disturbance behavior of blue sheep.

3.1 Disturbance source

Tourists and vehicles are the two main types of human recreational disturbance in SNFP. The reaction distance of wild animals is widely used to evaluate the level of threats that the target animal perceives [15,23]. The reaction distance of the three kinds of the animal response (i.e. N, V, F responses) showed significant differences between encountering tourists and vehicles. Reaction distances to tourists were larger then those to vehicles (Table 1). The MRLM confirmed that blue sheep kept higher vigilance to tourists by increasing the incidence of the V response>31 times (Table 4) and the F response>25 times (Table 5) when encountering tourists compared with vehicles. Further analysis revealed that the initiation distance of the F response to vehicles was significantly shorter than to tourists (Table 5). These analyses confirm that blue sheep are more tolerant to vehicles than to tourists.

Predictability of the disturbance source is one of the most significant factors in an animal's perception of predation risk [12]. Regular, repeated and non-threatening harassment may cause animals to become habituated [33,34], and thus to reduce the intensity of their reaction [4,13]. The fact that blue sheep were more habituated to vehicles than to tourists can be due to the fact that vehicles in the park move on fixed routes, while tourists are inclined to walk more randomly, which causes increased reaction in the sheep. Tourists take regulation SNFP sightseeing buses or other vehicles for tours around the park. Tourists in regulation buses are not allowed to get off the bus except for at observation decks set by SNFP. However, vehicles not belonging to SNFP also enter the park, and the behavior of tourists in these vehicles cannot be supervised. During the entire field research period, we recorded that tourists (numbers varying from two to five each time) got off vehicles randomly to observe and photograph at least twice per day. Typically, blue sheep did not appear disturbed when the vehicle stopped; however, they fled away once tourists disembarked from the vehicles.

3.2 Habitat

(1) Habitat types. Animals have the ability to learn to differentiate between dangerous and safe habitats. Features of different habitats represent different levels of threats, which lead to variation in anti-threat behaviors of wild animals [35]. For blue sheep, streams and ravines with open vegetation are the main habitat for drinking and foraging, while steep cliffs in mountains are used for resting and bedding [36]. Roads are built between ravines and mountains, where the two main types of human disturbance, tourists and vehicles, are concentrated. We observed the highest percentage of the F response when blue sheep were on roads (Table 1). The MLRM analysis further confirmed that the incidence of V and F responses were significantly higher on roads than in ravines or on cliffs. Nevertheless, blue sheep also showed the shortest vigilance and flight initiation distances on roads (Tables 4 and 5).

The larger F distance and higher incidence of alert behaviors (e.g. vigilance and flight) usually mean higher vigilance in animals [14,15,29,35]. Large herbivores could have shorter alert behavior (e.g. fright, flight, and running) distances in areas with heavy human activity, compared with populations that live with little human activity, due to their habituation to humans as reported in Svalbard reindeer (*Rangifer tarandus*) [37] and fallow deer (*Dama dama*) [24]. However, because a borderline of alert distance exists [37], a shorter human-blue sheep distance means closer to this borderline. Therefore, although reaction distances were shortest on roads, responses of blue sheep to disturbance were also most intensive on roads compared with the two other kinds of habitat (see HT in Tables 4 and 5). Meanwhile, to meet the needs of food and water, blue sheep frequently have to cross roads and move between feeding sites in ravines and resting sites on cliffs [36]. Stankowich mentioned that animals in areas with higher levels of human nonlethal disturbance showed reduced vigilance, and this phenomenon could be explained by a lack of alternative sites for the animal to move to [38]. Consequently, instead of avoiding roads, blue sheep strengthened their behavioral anti-disturbance strategy and become more habituated to human disturbance on roads compared with in ravines or on cliffs.

(2) Land cover. Ungulates typically use surrounding cover to avoid detection by predators [39], but in some circumstances, the dense cover could pose an impediment to their availability to detect predators and escape [40]. Consequently, ungulates have to tradeoff between the level of protective cover and perceptual constraints [38]. For example, mule deer flee more often in closed habitats [38,41,42], and antelopes and springboks (*Antidorcas marsupialis*) spend more time being alert with increasing vegetation height and cover, indicating the stronger risk of threat [43,44]. In this study we used the visibility index (VI) to evaluate the openness of the habitat used by blue sheep. MLRM found that blue sheep had higher potential to flee as the visibility index decreased, although the correlation between VI and the F distance was weak and not significant (Table 5). Liu et al. [36] reported that in summer, blue sheep tend to feed and rest in habitats characterized by mountain steppe zone, mountain open forest and steppe zone, where the height of trees and shrubs are low. We found that there was no significant difference of VI among the three categories of responses of blue sheep and between the tourist and vehicle groups (Table 1). The smallest mean visibility of blue sheep was 82% (VI=0.82) (Table 1), which means blue sheep always stayed in open areas with high visibility in this study. The low density of vegetation in the habitat may afford blue sheep better visibility for early detection of disturbance.

3.3 Behavior

(1) Head direction. Flight initiation distance (F distance) is one of the primary metrics in the study of risk assessment in ungulates [38]. The directness is usually determined by the angle between the approaching disturbance and the animal, which is correlated with the F distance of ungulates [45]. In this study, when blue sheep took a front head direction (HD), the approaching observer had the highest level of directness to the animal. Thus we recorded the highest significant incidence of flight behavior and the largest significant flight initiation distance (F distance) when HD of blue sheep was facing front (Table 5). We conclude that blue sheep kept the highest level of alertness when facing human disturbance front on.

(2) Population structure. Group size (GS), group type (GT), and gender (GEN) are the three most frequently used population variables when evaluating anti-disturbance behavior of ungulates [38]. Group size is always considered as a direct result of the anti-disturbance strategy of an ungulate species in a specific environment. However, the relationship between group size and alertness is also influenced by the group type and gender of members, since many studies have already found that females and females with young are usually more vigilant than males [46].

Although the dilution effect theory predicts that larger ungulate groups should exhibit less alertness [47], the results of empirical studies have been inconsistent. For example, Stankowich and Coss [23] found that larger groups had higher alertness than smaller groups in black-tailed deer, while MacArthur et al. [12] showed the reverse result, and many other studies showed no effect at all (see review by Stankowich [38]). In this study, we found that smaller groups were significantly more likely to flee than larger groups when disturbed by tourists (Table 1). However, this trend is likely to be weak since GS was not a significant variable in the final MLRM (Tables 4 and 5). Liu et al. [16] reported that the mean group size of blue sheep in less anthropogenically disturbed areas in Helan Mountains was 4.86±2.54 individuals and the largest group size was 51 individuals in summer. We observed the mean group size to be 3.7±3.1 individuals with the largest group of 26 individuals (Table 1). Manor and Saltz [15] found a negative relationship between group size and human disturbance. Smaller groups can be expected to show higher alertness because of higher *per capita* risk because of a lack of the "dilution effect" [38]. Consequently, the smaller group size in this study could be due to the need for higher *per capita* vigilance when staying in areas with high human disturbance.

Although both group type (GT) and gender (GEN) significantly influenced the alert behaviors of blue sheep (Table 1), only GEN entered the final MLRM (Table 3). Male blue sheep had a slightly higher ratio of vigilance response than females (*OR*=1.120), but V distances were not significantly different between the two genders (Table 4). On the other hand, males had significantly lower incidence of flight than females (*OR*=0.509), and the F distance of females were significantly larger than those of males (Table 5). Thus, we found that gender has a large effect on the decision to flee in blue sheep, and females are more wary of disturbance than males. This result is consistent with findings in other ungulate species [23,24,48,49]. The difference may be due to the distinct reproductive strategies between the two genders: males are less wary than females, especially when they are guarding or competing for mating with females, while females are most wary when they are guarding juveniles [50]. We recorded a total of 386 groups (times) of females in this study (Table 1). All were composed of female adults and at least one juvenile. Females increase their fitness by ensuring the survival of offspring, which could make them more likely to react to disturbance.

3.4 Suggestion

We found that blue sheep were more alert to tourists than to vehicles, and that roads caused the most intensive reaction of all habitat types, especially in females. Although we did not find any direct negative influence of tourists on blue sheep, we recommend that the behavior of tourists must be regulated to reduce human disturbance. Tourists should stay in vehicles or only be permitted to walk on footpaths and platform designed by SNFP. We also tested the alert behavior initiation distance of blue sheep, and our distance data can provide good reference material for SNFP to design or improve its walking facilities for tourists to balance the recreational needs of humans with the survival of blue sheep. Disturbance from recreation may have both immediate and long-term effects on wildlife [14,38]. Although we did not find direct negative influences of recreational disturbance on blue sheep, group sizes were smaller in high disturbance areas in this study compared with published group size data from areas with low human disturbance. We recommend that long term observations on the sexual structure, reproduction, and population trends of blue sheep should be conducted and compared with the populations in the Helan Mountains National Nature Reserve where human recreational activity is forbidden.

4 Conclusions

This study focused on the anti-disturbance strategy of blue sheep (*Pseudois nayaur*) towards human recreational disturbance in SNFP. Disturbance source (DS), habitat type (HT), visibility index (VI), head direction (HD), and gender (GEN) were the five significant variables influencing anti-disturbance behaviors of blue sheep. Of the two kinds of human disturbance, tourists and vehicles, tourists evoked stronger anti-disturbance reactions from blue sheep and were the main human disturbance to blue sheep in SNFP. Roads were areas with the most intensive human disturbance, and were also the areas that blue sheep have to cross everyday to meet the needs of food and shelter in ravines and on cliffs. Consequently, blue sheep became more habituate to human disturbance on roads than in the other two kinds of habitat by presenting the shortest alert distance and the highest reaction rates. Although group size, group type and gender are all possible population variables that can influence the anti-disturbance strategy of large herbivores, we found that only gender (GEN) caused a significant effect on blue sheep. Females were more vigilant than males by presenting significantly higher incidence of flight and longer flight initiation distance (F distance). In addition, open habitat and a front head direction towards the disturbance source provided blue sheep with the highest alertness and ability for rapid flight. Based on our findings, we suggest that SNFP balance the needs of blue sheep conservation biology with ecotourism by stricter regulation of the behavior of tourists. Meanwhile, the long-term population and behavioral ecology of blue sheep in SNFP should be studied and compared with the results of studies on other undisturbed blue sheep populations in the Helan Mountains.

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