Original Article

Interindvidual variability in habitat use: evidence for a risk management syndrome in roe deer?

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The way an individual reacts to the risk of predation or disturbance may have important consequences for its immediate and future survival. Risk is likely perceived differently by individuals in relation to among-individual differences in correlated behavioral traits, that is, syndromes or personalities. Given that animals can avoid the risk of predation/disturbance through modification of their habitat use, we might expect individuals of differing behavioral types to adopt contrasting tactics of habitat use when faced with risky or stressful situations. We studied the relationship between habitat use and among-individual variation in behavioral profile in a population of roe deer. We hypothesized that an individual’s habitat use tactics should be related to their capacity to cope with risky situations. In particular, we predicted that more reactive (risk-averse) roe deer, with relatively high behavioral response and high body temperature at capture, long flight distances and which were more vigilant during feeding, should use riskier open habitat less, particularly when risk is high. We found that although the use of open habitat during the day was negatively correlated with the indices of reactivity at capture, it was also positively correlated with indices of reactivity while foraging in open habitat. Furthermore, most of the behavioral parameters we measured were intercorrelated and moderately repeatable, potentially indexing personality traits. We conclude that there is substantial interindvidual variability in how individuals manage risky situations which imposes constraints on how they are able to exploit high-risk habitats, suggesting the existence of a risk management syndrome in this large herbivore.

Key words: behavior at capture, behavioral syndrome, body temperature, flight distance, risk-taking, vigilance.

INTRODUCTION

The capacity of individuals to cope with environmental variation may affect the persistence of populations, notably in human-modified landscapes (Dall et al. 2004). However, individuals of a given population often differ in their behavioral response to environmental perturbations, expressing contrasting tactics depending on their phenotypic traits and their sensitivity to stressors (Koolhaas et al. 1999; Martin and Réale 2008a). For example, some individuals are more aggressive, more active, bolder, or take more risk. These differences among individuals may reflect variation in animal temperament or behavioral syndrome, that is, consistent among-individual differences in a given behavior, or in suites of behaviors, over time and across contexts (Sih et al. 2004; Réale et al. 2010; Dingemanse et al. 2012).

Generally, such among-individual differences appear to vary consistently along a number of behavioral gradients, from individuals that are shy/risk-averse, less active, explore less and seek to minimize exposure to risk, to individuals that are bold/risk-taking, more active, explore more and are less sensitive to the risk of predation or disturbance (Sloan Wilson et al. 1994; van Oers et al. 2004; Koolhaas et al. 2007). For example, when faced with a given risk-related trade-off, certain individuals minimize risk by using safer habitats but, as a result, obtain only limited access to forage-rich habitats, whereas others prioritize the acquisition of high-quality resources but, therefore, may be subject to a higher degree of risk. In elk (Cervus elaphus), consistent among-individual differences have been observed in movement rates and risk-taking.
behaviors (use of open areas), resulting in a differential probability of surviving the hunting season: harvested individuals had bolder behavior, with higher movement rates and higher use of risky open habitat (Ciuti et al. 2012).

Although field examples are rare, it has been suggested that risk-taking is a component of a behavioral syndrome, as it is correlated with other behaviors such as dispersal or exploration (Fraser et al. 2001; Cote et al. 2010; Debeffe I, et al., unpublished data) and can have important consequences for individual fitness and population dynamics (Smith and Blumstein 2008; Möller and Garamszegi 2012; Sih et al. 2012). There is a clear need for field studies of interindividual variation in risk-taking behavior to better understand how these syndromes affect routine behavior such as habitat use (Archard and Braithwaite 2010; Dardenne et al. 2013).

Behavioral differences in risk-taking are often associated with physiological differences inherent to an individual’s behavioral tactic (“coping styles” sensu Koolhaas et al. 1999; Blas et al. 2007). Hence, interindividual variation in behavioral and physiological responses to a given disturbance or stressor are key components for defining personality or behavioral types (Koolhaas et al. 1999; Øverli et al. 2007). Many components of physiology and behavior may be affected by stress, for example, an increase in body temperature and heart rate is recognized as a typical component of the stress response (Korhonen et al. 2000; Carere and van Oers 2004), whereas an increase in the occurrence and/or duration of antipredator behavior such as vigilance is a typical response to a stressful situation (Wiepkema and Koolhaas 1993; Dwyer 2004). Shy or reactive individuals generally respond by expressing higher hypothalamic-pituitary-adrenal axis reactivity (i.e., a higher plasma corticosterone response and body temperature) but lower testosterone activity, characteristic of individuals with low activity and low aggression levels and that are less willing to take risks (Koolhaas et al. 1999). For example, in great tits (Parus major) bold individuals have lower body temperature and respiration rate during handling than shy individuals (Carere and van Oers 2004). Individual behavioral profiles, that is, among-individual variation in the behavioral and physiological response to stress, may impact both reproduction and survival. Even though many studies have documented interindividual differences in response to predation risk, for example, in terms of habitat use, little is known about the link between these differing responses and the behavioral profiles of individuals in the wild.

Increasing urbanization and agricultural intensification associated with an increase in ungulate populations, both in terms of their density and range across Europe (Apollonio et al. 2010; Morelet et al. 2011a), have led to increasing contact between human and wild ungulate populations. Human activities affect the survival and reproduction of wildlife (Boyce and Samson 1983; Knight and Gutzwiller 1995), so can be likened to a form of predation risk (Frid and Dill 2002). The European roe deer (Capreolus capreolus) has become the most abundant cervid across Europe, thriving in human-dominated agricultural landscapes (Hewison et al. 2001; Abbas et al. 2011). Moreover, as an income breeder (Andersen et al. 2000) with high daily energetic and nutrient requirements, the roe deer should be particularly sensitive to risks affecting its routine resource acquisition. In this study, we used the roe deer to investigate how within-population variability in patterns of habitat use may be related to differences among individuals in terms of their tolerance of disturbance.

In the landscape of fear (Laundre et al. 2001), habitat use should differ in relation to variations in perceived risk (Brown et al. 1999; Willems and Hill 2009) such that a higher global level of risk of predation/disturbance should provoke more marked modifications in habitat use. For example, we know that many wild ungulates use open habitat, with higher quality resources, mainly during nighttime and more closed habitat, with less forage but a higher degree of shelter, during daytime, when human disturbance is greater (e.g., Godvik et al. 2009; Bjornraas et al. 2011; Bonnot et al. 2013).

Because trade-offs among life-history traits may result in behavioral syndromes (Sih et al. 2004; Wolf et al. 2007; Luttheg and Sih 2010), we might expect to find a link between variation among individuals in habitat use tactics and their behavioral profile or syndrome. In particular, we might expect to observe interindividual variation in the use of high resource quality—high-risk habitats, particularly when disturbance is highest (e.g., during the day).

Here, with respect to the definition of behavioral syndromes, we first quantified and tested for consistency in among-individual variation, that is, repeatability, in the behavioral and physiological responses of roe deer to risk measured by body temperature and behavior at capture, as well as by flight distance and vigilance behavior during subsequent field observations performed during feeding bouts. Second, we hypothesized that roe deer habitat use should vary among individuals such that their exposure to high risk (i.e., use of open habitat during the day) varied in relation to their individual sensitivity to stress. To test this prediction, we analyzed patterns of habitat use of Global Positioning System (GPS) collared roe deer in a heterogeneous mixed-agricultural landscape and explored the link at the among-individual level between habitat use and behavioral profile indexed through the above behavioral and physiological measures. In particular, we predicted that more reactive individuals, with relatively high levels of behavioral response and high body temperature at capture, long flight distances, and which spent a high proportion of their time vigilant when foraging should use open habitat less during daytime (when anthropogenic disturbance is higher) compared with less reactive individuals. That is, we expected to observe interindividual variation in the use of open habitat during daytime, when the cost of foraging in open habitat is potentially high, but less, or none, during nighttime.

### MATERIALS AND METHODS

#### Study site

This study was carried out in a 12000 ha rural region in south-west France (N 43°17, E 0°53). It is a hilly area (elevation 260–380 m) with 2 large forests (672 and 463 ha) and numerous small forest patches (1265 patches; mean size of 1.5 ha, standard deviation = 4.0 ha, maximum area = 50.5 ha, covering 19.3% of the site). The remainder of the study site consists essentially of meadows for livestock grazing (37.2%), crops (31.6%), and hedgerows (3.6%). The crops commonly sown are cereals (sorghum, corn, wheat, barley), oilseed (sunflower, soy, rape), and fodder crops (alfalfa, ryegrass).

Human presence is high, distributed throughout the study site in small villages, farms, and isolated houses. An extensive road network covers the study site, but there are no major roads. Roe deer hunting occurs regularly from the second week-end of September to the end of January (or February since 2009), mostly using dogs for drive hunting. During summer, roe deer are also hunted by stalking. Roe deer density was estimated using a capture-mark-resighting approach (Hewison et al. 2007) to average 9.3 deer/100 ha in the mixed open landscape over the study period.
Data collection

Roe deer capture data
From 2003 to 2013, roe deer were caught during annual winter capture (November to March) using drive netting. Roe deer capture and marking procedures were approved by the French administration, taking into consideration animal welfare according to French law. Once a deer was caught, we removed it from the net and transferred it to a wooden retention box providing darkness and ventilation, but a minimum of space to minimize injuries and limit stress. Animals were kept in the retention box until they became calm, before beginning marking and physiological sampling. Most animals caught after 2008 were tranquilized with an intramuscular injection of acepromazine (calmivet 3 cc) (Montané et al. 2003). Each of the 319 individuals was weighed (with an electronic balance to the nearest 0.1 kg), sexed, aged (in 2 age classes: juveniles less than 1-year-old, and adults) and marked with 2 plastic ear tags.

From 2009, physiological and behavioral measurements were also recorded during capture to index the individual’s reactivity to the capture event. Reactivity to capture was determined for 167 individuals, some of which were equipped with a GPS collar (see below). For each individual at each capture (including individuals caught several times during consecutive annual captures), we measured its rectal temperature (with a Digitemp Color thermometer with a precision of 0.1 °C) at the beginning and at the end of the marking procedure and took the mean of these measures. As body temperature was measured during handling, this measure indexed the effect of stress-induced hyperthermia (i.e., the increase in body temperature in response to a stressful situation: Groenink et al. 1994; Korhonen et al. 2000; Carere and van Oers 2004). For the analysis, we removed one individual from the dataset with a very low mean temperature (36.9 °C) because it was clearly suffering from hypothermia (compared with the average rectal temperature of 38.9 ± 0.03), and a second individual because of a marked difference between the 2 temperature values (1.1 °C). We obtained both GPS data and body temperature data for 56 roe deer (Supplementary Appendix 1).

We also recorded the behavior of each individual during handling and release. Based on our extensive field observations of deer at capture, we considered a priori that certain behaviors were clearly indicative of reactive individuals (sensu Koelhhas et al. 1999) that had difficulty coping with this stressful event. Hence, we attributed a score of 1 (otherwise 0) for each of the following behaviors: if the individual struggled in the net (see also Réale et al. 2000), if it turned upside down in the box, if it attempted to remove its collar at release and if it fell (i.e., stumbled and fell to the ground) at release. In addition, we attributed a score of 1 if the individual struggled and panted on the table during marking, or a score of 0.5 if it struggled only (otherwise 0), and a score of 1 (high speed running), 0.5 (moderate running), or 0 (trotting) in relation to its flight behavior at release. Indeed, flight speed at release is commonly used to index behavioral reactivity with a precision of 0.1 °C for FID. Because all observations were performed in open habitat, we assumed that variation in predation risk and resource quality across observations was minimal and random with respect to the identity of the individual observed. No individual was observed more than once a day.

Focal sampling. To study variation among individuals in behavioral profile in relation to the baseline level of predation risk and/or disturbance in our study site, we monitored the vigilance behavior of individually marked undisturbed foraging roe deer. We recorded 6 exclusive behaviors: vigilance (head above shoulder level while scanning surroundings), feeding (collecting food, or searching for food with head at ground level), head raised (head above shoulder level but without scanning), moving (walking or trotting, head above shoulder level), grooming, and “others.” The majority of the observations (around 70%) were collected at dawn and dusk, during peak activity for roe deer (Jeppesen 1989). After locating and identifying the focal individual by radio tracking, we observed its behavior using binoculars (10 × 42) and recorded behavioral sequences on a numeric recorder for at least 3 min. Observations ceased when the focal individual was no longer visible or lay down, when the observer was detected by the deer, or after approximately 10 min of observation.

We analyzed the behavioral sequences using behavioral observation transcription software (EthoLog 2.2; Ottone 2000). The roe deer has relatively short activity phases (e.g., Turner 1979), such that a feeding bout may be followed by other types of activity (walking, grooming, etc.) within short intervals of time. Because we wanted to focus on variation in how individuals managed risk through vigilance behavior, we exclusively selected feeding phases within each behavioral sequence. We defined a feeding phase as a succession of different behaviors (e.g., vigilance, feeding, grooming, ...) containing at least 2 feeding behaviors (at the start and the end of the phase) with no interruptions (i.e., nonfeeding behavior) that lasted more than 60 s. That is, if a roe deer engaged in nonfeeding behavior during 60 s or more, it was considered as being involved in a different type of phase (e.g., a moving or a grooming phase) and so that phase was not considered here. Therefore, a given behavioral sequence could include one or several feeding phases. Then, we calculated the proportion of time spent on each behavior during feeding phases of each behavioral sequence. Because we had repeated observations for all individuals, we calculated the mean proportion of time spent vigilant over all observations for a given individual. Because sampling effort was not equal across individuals, we weighted means by sample size for each individual. We obtained both GPS and focal time-budget data for 25 individuals (Supplementary Appendix 1).

Flight initiation distance. To study variation among individuals in their behavioral response to a stressful event, we measured FID (the distance between the predator/observer and the target animal...
when it takes flight; Ydenberg and Dill 1986; Stankowich 2008). That is, following identification of the focal individual, the observer walked toward the roe deer at normal walking pace while a second observer noted the animal’s behavior and communicated this to the approaching observer using walkie-talkie. The points when the roe deer became vigilant and when it took flight were marked by the approaching observer using flags pushed into the ground. Hence, using a rangefinder or a tape measure, we could subsequently measure: the total distance between the initial position of the animal and the initial position of the observer, and the FID, that is, the distance between the approaching observer and the animal when it took flight. As far as possible, we tried to standardize conditions during these observations by initiating the approach when the focal animal was side-on and engaged in a feeding phase, with its head above shoulder level, and at a lower altitude than the initial position of the observer. We ensured that the total distance between the observer and the initial position of the focal individual was never inferior to 100 m. Because we obtained repeated measures of FID for individually marked deer (between 1 and 6 observations), we calculated mean FID over all observations for a given individual. In our study site, roe deer were frequently disturbed by human activities, we therefore supposed that habituation of monitored roe deer to the FID protocol was negligible. Because sampling effort was not equal across individuals, we weighted means by sample size for each individual. We obtained both GPS and FID data for 21 individuals (Supplementary Appendix 1).

Telemetry and GPS data
From 2003 onward, 243 roe deer were equipped with a GPS collar (12 channel Lotek 3300 GPS or GSM). Collars were programmed to obtain the location of the roe deer with a schedule of 1 GPS fix every 4 hours (at 04:00, 08:00, 12:00, 16:00, 20:00, and 00:00 h for the first 2 winters, that is, 2003 and 2004) or every 6 hours (at 06:00, 12:00, 18:00, and 00:00 h for the following winters). We performed differential correction in order to improve fix accuracy (Adrados et al. 2003). Even though some individuals were caught and equipped with a GPS collar several times, we included a maximum of one GPS monitoring year per individual in our analyses.

Because we expected that individuals should adopt different habitat use tactics in relation to their behavioral profile, we determined habitat use in fall during hunting, when human-induced disturbance should be particularly high. That is, we determined habitat use over a period of approximately 9 weeks (from 2 weeks after the start of the hunting season until the end of December, or until GPS monitoring ceased). To evaluate habitat use during the day and during the night, we used 2 GPS fixes per 24 h: at 12:00 h to characterize daytime habitat use and at 00:00 h to characterize nighttime habitat use. Because roe deer are highly sedentary (Strandgaard 1972, Hewison et al. 1998), we supposed that individuals were consistent in their habitat use over years. Hence, for some individuals (N = 4), GPS data and physiological and/or behavioral data were sampled one or more (maximum = 4) years apart (see Supplementary Appendix 1). Repeating the analysis with or without these individuals did not change our results or conclusions (data not shown), hence, we retained these individuals for the following analyses.

For the analysis, we removed GPS fixes for which the location was obviously aberrant (i.e., fixes that would imply an unfeasible movement speed given the distance from the previous or to the next location). We also removed pure “forest” individuals (N = 14), caught in 1 of the 2 large massifs of the study site (Figure 1), because they spent almost all of their time in woodland (83% on

![Figure 1](https://academic.oup.com/beheco/article-abstract/26/1/105/2262108/108) Map of the study site illustrating landscape heterogeneity. Two large forest massifs and other fragmented patches of woodland and hedgerows are depicted in black. Open habitats (crops, meadows...) are depicted in white. Gray patches represent open water.
average), therefore, there could not be any day–night contrast in their habitat use at the landscape scale.

**Statistical analyses**

**Repeatability estimates**

Individual behavioral consistency was assessed by calculating repeatability estimates on measures of each index of reactivity using mixed models (Nakagawa and Schielzeth 2010). Repeated measures of body temperature and behavioral score were obtained from yearling or adult individuals that were caught more than once between 2009 and 2013 (i.e., 17 individuals were sampled at least twice during capture; body temperature = mean of 2.35 measures/individual; behavioral score = mean of 2.41 measures/individual, Supplementary Appendix 1). Repeated measures of time spent vigilant and FID were obtained from individuals observed several times during the falls of 2010 and/or 2011 (i.e., 23 individuals for time spent vigilant; mean of 4.13 observations/individual; 21 individuals for FID; mean of 3.52 observations/individual, Supplementary Appendix 1). Repeatability estimates were based on data from all individuals caught at least twice since 2009 (for body temperature and behavioral score at winter capture) or observed at least twice during fall 2010 and 2011 (for FID and proportion of time spent vigilant) (Réale et al. 2007). Prior to the estimate of repeatability coefficients, we log-transformed the FID variable to achieve normality.

Repeatability coefficients, that is, intraclass correlation index, were calculated using the “rpt, remiLMM” function of the “rptR” package (Schielzeth and Nakagawa 2011) in R software (with R software version 2.13.1; R Core Team 2012), which estimates repeatability as the ratio of between-individual variance to total variance with linear mixed-effects models (with individual identity as a random factor) using the restricted maximum likelihood method. For the “time spent vigilant” variable only (i.e., the proportion of time spent vigilant in relation to the total duration of each behavioral phase, varying between 0 and 1), we calculated the repeatability coefficient with the “rpt.binomGLMM.multi” function of the “rptR” package using a generalized linear mixed-effects models with a logit-link.

**Correlations among indices of reactivity**

We tested for correlation among all indices of reactivity using a Spearman’s rank correlation. We used the “spearman.test” function in the “pspearman” package (Vivian 2009) in R software to obtain the correlation matrix between body temperature, behavioral score, FID, and time spent vigilant (Table 1).

**Habitat use**

Because we expected to observe interindividual variation in the use of open habitat, but mostly during daytime when the risk of predation or disturbance is higher, we contrasted the use of open habitat during daytime and nighttime for each individual. For this, we calculated the probability of being in open habitat during daytime and during nighttime (see Equation 1 below). Open habitat was defined as those habitat types that were not forested or hedgerows and consisted mainly of crops, meadows, and scrubland (see Morellet et al. 2011b, for more details on the spatial data processing). To compare individual daytime habitat use to nighttime habitat use, we retained only those individuals that did not have an overly marked difference in the number of fixes between daytime and nighttime (Bonnot et al. 2013); that is, we discarded 4 individuals with a marked sampling imbalance in terms of the number of fixes recorded during daytime compared with nighttime (i.e., the number of fixes available during daytime was, on average, equivalent to 30% of the number of fixes available during nighttime).

\[
P_{\text{open}}(\text{day (or night)}) = \frac{\text{Number of locations in open habitat during daytime (or nighttime)}}{\text{Total number of locations in any habitat during daytime (or nighttime)}}
\]

We used generalized linear mixed models to investigate variation in use of open habitat in relation to the period of the day (daytime or nighttime) and in relation to interindividual variation in behavioral profile indexed by rectal temperature, behavioral score (during capture), the proportion of time spent vigilant, and the FID (during fall observations). We included individual identity as a random factor because we had repeated measures for daytime and nighttime. Because our dependent variable was the probability of being in open habitat \((P_{\text{open}})\) (vs. the probability of being in closed habitat, \((1 - P_{\text{open}})\)), we used generalized linear mixed models with a binomial distribution and a logit link. We constructed 4 sets of generalized linear mixed models, one for each of the indices of reactivity (proportion time spent vigilant, FID, body temperature, and behavioral score). For each reactivity index, because we expected that the contrast in the use of open habitat between day and night should be linked to the individual’s behavioral profile, we compared the model with the 2-way interaction between the period of the day (2 modalities: daytime and nighttime) and the reactivity index (continuous) with the model including the fixed effect of these 2 variables, but not their interaction, with the 2 models including only 1 of these 2 effects and with the constant model (Table 2). For each reactivity index, we used the second order Akaike’s information criterion corrected for small sample size (AICc; Burnham and Anderson 1998) and Akaike weights to select the model with the most support among the models constructed a priori (Table 2). The model with the lowest AICc value reflects the best compromise between precision and complexity. We also retained and discussed models with an AICc value differing by <2 from that of the best model.

All generalized linear mixed models were fitted using the “lmer” function in the library “lme4” (Bates et al. 2011) implemented in R software. We used the “aictab” function in the library “AICcmodavg” (Mazerolle 2011) to perform model selection.

**RESULTS**

**Repeatability**

Body temperature at capture was highly repeatable for a given individual (\(r = 0.44, 95%\) confidence interval [CI] = 0.04, 0.72) and behavioral score was moderately repeatable (\(r = 0.20, \text{CI} = 0, 0.56\)). In contrast, FID and the proportion of time spent vigilant were
not repeatable for a given individual (respectively, FID: \( r = 0.08, \) CI = 0, 0.30; vigilance: \( r = 0, \) CI = 0, 0.01). Note that there was no variation in the proportion of time spent vigilant or FID in relation to trial order for a given individual, indicating that deer did not become habituated to our experimental protocol for measuring these behaviors (results not shown).

**Correlation among indices of reactivity**

The correlation matrix using Spearman’s rank correlation showed that some of the reactivity indices were intercorrelated (Table 1). Body temperature was positively correlated with the behavioral score and with FID, whereas time spent vigilant was weakly negatively correlated with the behavioral score.

**Use of open habitat in relation to behavioral profile**

For those individuals for which we had both GPS data and behavioral profile data, body temperature varied from 37.5 to 40 °C (with an average of 38.9 °C; \( N = 56 \)), the behavioral score varied from 0.08 to 0.75 (with an average of 0.27; \( N = 58 \)), the proportion of time spent vigilant varied from 8% to 51% (with an average of 23%; \( N = 25 \)), and FID varied from 77 to 198 m (with an average of 141 m; \( N = 21 \)).

To test the hypothesis that individuals adjust their use of open habitat in relation to their reactivity to a stressful situation, we performed model selection on 4 sets of generalized linear mixed models, one for each reactivity index. As shown in Table 2, the best model for behavior at capture contained the 2-way interaction between the period of the day and behavioral score (AICc weight = 1). We obtained similar results whether we considered the behavioral score as the average of the 6 behavioral items at capture (Table 2, Figure 2a) or as the principal components from the PCA of those same items. Notably, we found a significant relationship between the use of open habitat during the day and the second component of the PCA, describing individuals that turned upside down in the box and had a high running speed at release (results shown in Supplementary Appendix 2). That is, the probability of being in open habitat during daytime decreased with increasing values of the behavioral score (i.e., a higher probability of turning upside down in the box, struggling, panting, falling, and with a higher running speed at release) (Figure 2a). Indeed, less reactive individuals at capture, with low behavioral scores, had a probability of around 40% of being in open habitat during daytime, whereas individuals with high behavioral scores had a probability of around 20% of being in open habitat during daytime. In contrast, the probability of being in open habitat during nighttime was higher and tended to increase very slightly with increasing behavioral score. In the same way, the best model for rectal temperature included the 2-way interaction between temperature and the period of the day (AICc weight = 0.63). That is, the probability of being in open habitat during the daytime decreased with increasing rectal temperature, but was higher and relatively invariable during nighttime (Figure 2b). However, the model including the additive effects of the period of the day and temperature also had some support, as the AIC value for this model was very close to that of the best model (ΔAICc = 1.10, AICc weight = 0.37).

Concerning the relationships between habitat use and vigilance on one hand and flight distance on the other hand, the best models explaining the probability of being in open habitat included the 2-way interactions between the period of the day and time spent vigilant (AICc weight = 1.00) and the period of the day and FID (AICc weight = 0.98), respectively (Table 2). The probability of being in open habitat during daytime increased with increasing values of FID, but was higher and relatively invariable during nighttime (Figure 2c). That is, individuals with short FIDs spent 20% of their time in open habitat during daytime (and around 85% during nighttime), whereas individuals with long FIDs used open habitat as much during daytime as during nighttime (i.e., they spent around 50% of their time in open habitat during the day and during the night). Similarly, the probability of being in open habitat during the daytime increased slightly with an increase in the proportion of time spent vigilant, but was also higher and decreased slightly during nighttime (Figure 2d). Confirming this pattern, we also found that the probability of being in open habitat during the daytime decreased with an increase in the proportion of time spent feeding, whereas it was higher and increased slightly during nighttime (model selected: 2-way interaction between the time of day and time spent in feeding with an AICc weight = 1.00; Supplementary Appendix 3). These results were generally robust to the inclusion of other individual attributes (sex, age, body mass) in the models (see Supplementary Appendix 4), and also when we restricted the analyses to the 21

### Table 2

**Summaries of the candidate generalized linear mixed models to investigate the probability of being in open habitat in relation to the 4 indices of individual reactivity: body temperature (\( N = 56 \)), behavioral score (\( N = 58 \)), proportion of time spent vigilant (\( N = 25 \)), FID (\( N = 21 \))**

<table>
<thead>
<tr>
<th>Models</th>
<th>Temperature</th>
<th>Behavioral score</th>
<th>Vigilance</th>
<th>FID</th>
</tr>
</thead>
<tbody>
<tr>
<td>Day period × reactivity index</td>
<td>5</td>
<td>551</td>
<td>0</td>
<td>0.63</td>
</tr>
<tr>
<td>Day period + reactivity index</td>
<td>4</td>
<td>552</td>
<td>1</td>
<td>0.37</td>
</tr>
<tr>
<td>Reactivity index</td>
<td>3</td>
<td>577</td>
<td>26</td>
<td>0</td>
</tr>
<tr>
<td>Day period</td>
<td>3</td>
<td>2677</td>
<td>2126</td>
<td>0</td>
</tr>
<tr>
<td>Constant</td>
<td>2</td>
<td>2640</td>
<td>2088</td>
<td>0</td>
</tr>
</tbody>
</table>

These models included the given reactivity index and the period of the day ("Day period"; daytime vs. nighttime). All models specified with a 2-way interaction also include main effects. AICc is the value of the corrected Akaike’s information criterion and \( K \) is the number of estimated parameters for each model. The ranking of the models is based on the differences in the values for ΔAICc and Akaikes weights (\( w \)). For each reactivity index, the most parsimonious model is given in bold.
individuals common to the 4 metrics used to index behavioral profile (see Supplementary Appendix 5).

**DISCUSSION**

In this study, we demonstrated a link between an individual’s behavioral profile and its willingness to take risk by using open habitat during daytime. This was the case whether we measured behavioral sensitivity to stress during a highly stressful event (i.e., capture), or during normal ranging activities (describing the individual’s response to a baseline level of risk). We have previously shown that roe deer habitat use in heterogeneous landscapes is, on average, constrained by human activities (Coulon et al. 2008; Bonnot et al. 2013, in the same study site). The present results demonstrate that individuals vary in their habitat use tactic around this population mean in relation to their individual sensitivity to stress.

In our study population, we hypothesized that individuals should react differently to the risk associated with the use of open habitat depending on their individual tolerance of stress associated with risky situations. Overall, our results showed that interindividual variation in the day–night contrast of using open habitat was related to all 4 descriptors of behavioral profile to varying degrees: the behavioral score and body temperature at capture (Figure 2a,b), and the distance at which an individual takes flight in response to human disturbance (FID) and the proportion of time spent vigilant during feeding bouts (Figure 2c,d). These results suggest that an individual’s willingness to confront risk or disturbance determines its tendency to use open habitat during the day, but in 2 contrasting ways. As expected, individuals with a marked response to a highly stressful event (relatively high temperature and high behavioral score), in our case capture, used open habitat less, especially during daytime, when anthropogenic disturbance is highest, compared with individuals that were less reactive during the capture event (relatively low temperature and low behavioral score). However, on the other hand, and in contrast to our expectations, individuals which were a priori more reactive during normal activities, expressing a stronger response to disturbance while foraging in open habitat (relatively long FIDs and spending more time vigilant), used open habitat more during daytime compared with the a priori less reactive individuals. Thus, these 2 gradients of behavioral profile, one measured during capture, the other during normal foraging activities, appear to describe different components of the behavioral response to human disturbance.

One possible explanation for these results is that the increase in antipredator behaviors such as FID and vigilance among roe deer that usually use open habitat during the day is the result of the adaptation of roe deer to riskier open habitat, following its relatively recent colonization of fragmented landscapes (Hewison et al. 2001). Under this hypothesis, intrinsic differences in personality or behavioral types could cause individual roe deer to use different habitats depending on the associated level of risk. As a result, individuals that are able to express an appropriate response to habitual disturbance would be more likely to use open habitat more during daytime. In contrast, individuals that are highly reactive when confronted with an unusually stressful event such as capture would be unable to deal with habitual sources of disturbance and, therefore, mostly confine their space use to closed protective habitats during the day when such disturbance events are common. This interpretation remains, however, somewhat speculative given the lack of repeatability of the FID and vigilance measures in our

**Figure 2**

The probability of being in open habitat during daytime (gray) and nighttime (black) in relation to (a) behavioral score at capture ($N = 58$), (b) body temperature ($N = 56$), (c) FID ($N = 21$), and (d) proportion of time spent vigilant ($N = 25$), shown with 95% CIs (dashed lines).
study, probably due to the low sample size and higher sensitivity of these behaviors to environmental variation (see below). A second hypothesis is that the higher levels of antipredator behaviors observed among certain individuals are the result of significant behavioral plasticity in response to higher risk. In this case, individuals that usually use open habitat during daytime compensate for their risk-taking by increasing their antipredator behavior. In this case, individual behavioral responses would be a consequence of the different levels of risk experienced by individuals depending on their exposure to disturbance through use of open habitat. It is difficult to distinguish between these 2 explanations without explicitly analyzing variation in antipredator behaviors of a given individual across varying environmental contexts (i.e., behavioral reaction norms, *sensu* Dingemans et al. 2010; see Mathot et al. 2011). However, all our observations of FID and vigilance were recorded in risky open habitat and it seems reasonable to assume that there was no systematic bias in terms of environmental context (i.e., risk and/or resources) among observations for different individuals. Whatever the causes of the observed relationship between the propensity to take risks and the expression of antipredator behaviors, we found that individuals used open habitat differently depending on their behavioral profile.

Our interpretation is supported by certain estimates of repeatability calculated for each index of reactivity. Indeed, if the gradient of risk-taking that we identified does, indeed, translate into among-individual variation in temperament, the behavioral components should be repeatable across contexts and over time (Réale et al. 2007). In a meta-analysis, Bell et al. (2009) found an average repeatability of behavioral traits of 0.37. In this study, body temperature was highly repeatable (*r* = 0.44), whereas the behavioral score at capture was moderately so (*r* = 0.20). In contrast, time spent vigilant and FID were not repeatable. However, vigilance and FID behaviors are generally considered as important components of animal temperament and are commonly used to determine the existence of behavioral syndromes or personalities, particularly in ungulates and birds (e.g., Bergwall et al. 2011; Couchoux and Cresswell 2012). Because repeatability estimates vary greatly between different classes of behavior (Bell et al. 2009), we suppose that vigilance and FID behaviors are more sensitive to environmental context (Couchoux and Cresswell 2012) and, hence, are somewhat more variable for a given individual. However, a greater number of repeat observations per individual would be required to assess whether among-individual variation in the degree of plasticity (Dingemans et al. 2010; Mathot et al. 2012) of antipredator behaviors such as vigilance and FID constitutes an important component of animal personality in the wild.

Overall, our study suggests that there is substantial interindividual variation in how animals manage the risk associated with being in open habitat and could be linked to the concept of behavioral syndromes. This hypothesis is supported by the fact that several physiological and behavioral traits that we measured were intercorrelated, suggesting a degree of consistency in the response of a given individual to risk across different contexts and, hence, a behavioral syndrome. Behavioral syndromes are considered to be highly correlated to the stress responses of individuals (Korhonen et al. 2000; Carere and van Oers 2004; Martin and Réale 2008a, 2008b) and are predicted to cause animals to distribute themselves in a nonrandom way in response to human disturbance. Our results suggest that roe deer individuals with a risk-tolerant behavioral profile expose themselves to greater risk (related to human activities) by using open habitat during the daytime to a greater extent than more sensitive individuals. We speculate suggest that these risk-tolerant deer can be considered as “bold” individuals which are known to be less fearful and more likely to take risks (e.g., Sloan Wilson et al. 1994; Boissy 1995; Wilson and Godin 2009). Conversely, deer that avoided open habitat during the day, thus exposing themselves less to risk, could be considered as “shy” individuals. Similarly, Martin and Réale (2008a) showed that more explorative and docile chipmunks (*Tamias striatus*) were more common in areas with levels of high human presence. However, some caution is warranted in this interpretation, because behavioral syndromes are generally defined as a suite of correlated behaviors describing among-individual consistency in behavior over time and across situations (Sih et al. 2004; Stamps and Groothuis 2010). Although some physiological and behavioral components that we measured during capture do appear to be repeatable to some extent (see above), further information is required to confirm this hypothesis.

Our study has shown that the spatial behavior of a large wild herbivore is constrained by both human activities and interindividual variability in how individuals manage risk. There is a pressing need for further studies that attempt to relate interindividual variability in behavior in the wild to behavioral syndromes (Archard and Braithwaite 2010) in order to better document variation in the responses of wildlife to human activity. This could help to better understand how animals may adapt to human-induced changes of their environment, but also to the recent return of large predators across much of Europe (see Lone et al. 2014). The impact of such contrasting or cumulating selective pressures in multipredator landscapes could influence the distribution of behavioral types among habitats and requires further study.

**SUPPLEMENTARY MATERIAL**

Supplementary material can be found at [http://www.beheco.oxfordjournals.org/](http://www.beheco.oxfordjournals.org/)

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