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The link between behavioural type and natal dispersal propensity reveals a dispersal syndrome in a large herbivore

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When individuals disperse, they modify the physical and social composition of their reproductive environment, potentially impacting their fitness. The choice an individual makes between dispersal and philopatry is thus critical, hence a better understanding of the mechanisms involved in the decision to leave the natal area is crucial. We explored how combinations of behavioural (exploration, mobility, activity and stress response) and morphological (body mass) traits measured prior to dispersal were linked to the subsequent dispersal decision in 77 roe deer *Capreolus capreolus* fawns. Using an unusually detailed multi-trait approach, we identified two independent behavioural continuums related to dispersal. First, a continuum of energetic expenditure contrasted individuals of low mobility, low variability in head activity and low body temperature with those that displayed opposite traits. Second, a continuum of neophobia contrasted individuals that explored more prior to dispersal and were more tolerant of capture with those that displayed opposite traits. While accounting for possible confounding effects of condition-dependence (body mass), we showed that future dispersers were less neophobic and had higher energetic budgets than future philopatric individuals, providing strong support for a dispersal syndrome in this species.

1. Introduction

Natal dispersal, defined as the net movement between the natal area and the site of first breeding [1], is a fundamental life-history trait and a complex phenomenon influenced by multiple factors [2–4]. Natal dispersal has important consequences at the individual level for survival and reproduction over the lifetime [5,6], and at the population level for gene flow, spatially structured population dynamics and invasion capability [2–4]. Understanding the ultimate and proximate factors that affect dispersal is thus of primary interest. In most populations, not all individuals of a given sex disperse and dispersing individuals are generally not a random subset of the population [2,7]. Indeed, the decision an individual makes to stay on or leave the natal area may be condition-dependent [2], potentially linking dispersal outcomes with environmental context (e.g. habitat quality or heterogeneity) and/or individual attributes. For instance, dispersers have been found to have higher corticosterone levels in screech-owls *Otus asio* [8] or to be heavier [2,9], as reported in ground squirrels *Spermophilus beldingi* [10] and Eurasian eagle-owls *Bubo bubo* [11]. Together, the suite of individual attributes which are correlated with dispersal in a given population or species is defined as a dispersal syndrome [4]. To date, only a few studies have identified dispersal syndromes [4,12] and no study to our knowledge has provided evidence for a behavioural syndrome of dispersal while simultaneously accounting for possible confounding effects of condition-dependence. We aimed to fill the gap in this paper by assessing the link between a suite of behavioural traits measured prior to dispersal, a reliable index of individual condition (body mass) and the subsequent decision whether or not to disperse using an intensively studied population of large herbivore as a model.

Interest in the study of behavioural differences among individuals has increased tremendously over recent years [13,14]. Indeed, the existence of different temperaments, personalities or behavioural syndromes has been investigated in a large variety of taxa [13]. Personalities can have a profound impact on life-history traits [14,15] and several studies have demonstrated a link between personality and fitness [5,6]. For example, bold bighorn sheep *Ovis canadensis* ewes reproduce earlier and have higher weaning success than shy ones [6], while in the common lizard *Lacerta vivipara* socially tolerant individuals grow faster and reproduce better [5].

Dispersal may also be associated with personality traits, potentially providing insights regarding the mechanisms underlying the decision to leave the natal area. For instance, boldness is positively linked to dispersal distance in the Trinidad killifish *Rivulus hartii* [16], while dispersers are faster explorers than philopatric individuals in great tits *Parus major* [17]. Similarly, bank voles have higher general levels of activity in colonizing populations than voles in more stable populations [18]. Finally, differences in social profile are related to the dispersal decision in lizards [19] and in great tits [20]. In particular, in bluebirds *Sialia mexicana* and *Sialia currucoides*, highly aggressive males are more common on the invasion front [21]. However, while these studies have provided evidence that some personality traits do influence dispersal, they did not address the question of whether dispersal propensity is associated with a behavioural syndrome independently of condition-dependence [12]. Indeed, the vast majority of studies on personality-dependent dispersal have focused on a single behavioural trait, while the three that used a multi-trait approach were carried out under laboratory conditions and did not account for possible confounding effects of condition-dependence [22–24]. The use of a multi-trait approach while correcting for possible condition-dependence provides the most robust way to test for the existence of a behavioural syndrome associated with dispersal propensity.

To address the above question, we explored how combinations of behavioural and morphological traits measured prior to dispersal were linked to the subsequent dispersal decision in a wild large herbivore. We first tested for the existence of a behavioural syndrome (i.e. inter-correlation among several behavioural traits) prior to natal dispersal in a free-ranging population of roe deer *Capreolus capreolus*, and then investigated whether inter-individual variation in this behavioural syndrome was correlated with natal dispersal behaviour while accounting for condition-dependence. Roe deer are medium-sized, slightly dimorphic and weakly polygynous mammalian herbivores that are widely spread across Europe [25]. Natal dispersal is not sex-biased in this species [26–28], but heavier fawns disperse more frequently, earlier and further than lighter fawns, while fawns in pure forest disperse less than those in more heterogeneous habitats [27]. We controlled for this condition- and habitat-dependence while exploring the link between dispersal propensity and a suite of four behavioural traits (exploration, mobility, activity and stress response), encompassing three of the five major components of personality that are commonly recognized [29] (i.e. exploration, activity and boldness). We tested the hypothesis that dispersers should be of a particular behavioural type (i.e. a particular type of individual, as measured prior to the dispersal period) which should differ from that of philopatric individuals because specific morphological, physiological and behavioural traits may be required to minimize dispersal costs [12]. In particular, we expected a dispersal syndrome in roe deer such that, prior to natal dispersal, dispersers should engage in more exploratory behaviour, be more mobile and more active, and have a less pronounced stress response compared with philopatric individuals.

2. Material and methods

(a) Study area

The study was conducted in a hilly (260–380 m.a.s.l.) and heterogeneous agricultural landscape (N 43°27′, E 0°85′) covering around 10 000 ha in southwest France. The area is a mixed landscape of open fields and small woodland patches (average size of 3 ha) dominated by oak *Quercus* spp., with 23.7% woodland, 36.1% meadows, 32.1% cultivated fields and 4.3% hedgerows. We identified two sectors of contrasting landscape structure based on woodland extent [30]. The first sector was made up of two forest blocks, whereas the second sector was composed of a more open landscape of fragmented woodland [30].

(b) Capture, handling and monitoring

Roe deer were caught from 2002 to 2013 during winter (from 16 November to 27 March) using drive netting. For each animal, we recorded its body mass to the nearest 0.1 kg and its sex, and we attributed an age class before fitting it with a collar and releasing it on site. Fawns (less than 1 year old) are distinguishable from older deer by the presence of a tri-cuspid third pre-molar milk tooth [31]. Since 2009, for each individual caught, behaviour at capture (detailed below) was also recorded. During the 10 winters of sampling, 127 fawns (6–10 months old) were captured and equipped with a Lotek 3300 GPS or a Lotek Small WildCell GSM collar. Collars were programmed to obtain a location every 4 h (in 2002–2004) or every 6 h (in following years) over approximately 11 months. Since 2005, and for Lotek 3300 GPS collars only, around 12 intensive monitoring periods of one location every 10 min for 24 h spaced across the year were also programmed. We performed differential correction to improve fix accuracy [32]. GPS collars also provided information on activity through two head position sensors [33]. GPS data were recovered for 102 fawns. Capture and handling induce transient modification of roe deer behaviour, hence the location data for the first week after release were excluded from the analysis [34]. All capture, handling and collaring were done according to the French law for animal welfare and procedures were approved by the French administration.

Roe deer fawns disperse in spring [35] and the timing of dispersal is highly synchronized [27,36], so that their dispersal status can be accurately determined by the end of May. Therefore, of the fawns captured and for which data were recovered, only those individuals monitored from their first capture in winter to at least the end of May and with a minimum average of two GPS locations per day were retained for subsequent analyses ($n = 77$; mean percentage of missing values $= 10.3\% \pm 10.4$, min $= 0\%$, max $= 46.2\%$); body mass at capture was not recorded for one individual. Note that although four (two sets of two) of these 77 individuals were litter-mates, the results reported below were robust to their inclusion (not shown).

(c) Defining philopatry versus natal dispersal

Natal dispersal was defined as permanent emigration from the natal range (pre-dispersal home range) to a distinct adult range (post-dispersal home range) where the first breeding event occurs such that pre-dispersal locations did not overlap post-dispersal locations [37]. As described in Debeffe *et al.* [27], we used the range stability index of Roshier & Reid [38] to discriminate dispersers from philopatric animals.

Five fawns exhibited a dispersal-type movement (travelling an average of 17.66 ± 10.03 km), but then returned sometime later during summer (average 11.46 ± 11.88 weeks) to their natal range. Although these five pseudo-dispersing fawns probably reproduced for the first time within their natal home range, for subsequent analyses they were considered as dispersers as they left their natal area during the dispersal period for a substantial duration. Hence, we assumed that the individual behavioural characteristics associated with this movement were the same as, or similar to, those for true dispersal movements, even though this attempted dispersal was subsequently aborted. Excluding pseudo-dispersal events from the analyses did not change the results (not shown).

(d) Behavioural traits

(i) Exploratory movements

Extra-range movements were defined as short-term trips made outside of the individual's normal home range and were assumed to translate an individual's willingness to explore novel environments. To detect extra-range movements prior to dispersal, hereafter called explorations, we first calculated the 95% fixed kernel home range and then defined an exploration as at least two successive locations outside of this pre-dispersal range (because a single outlying location may be due to GPS error [39]). The number of explorations performed during approximately three months before the dispersal period (i.e. between January and the date of dispersal) and the total distance travelled during exploration were determined for each GPS monitored fawn ($n = 77$) [39]. The total distance travelled during exploration was correlated with the maximum distance to the barycentre of the home range during exploration (linear regression: $n = 39$, $r^2 = 0.71$, d.f. $= 37$, $F = 89.11$, $p < 0.001$), indicating that individuals did not necessarily stay in the vicinity of their home range while exploring.

(ii) Mobility

We estimated mobility prior to dispersal at two scales: (i) the home range scale (using the base-level monitoring of one GPS location every 4 or 6 h during 60 days prior to dispersal initiation, or a threshold date randomly chosen from the distribution of dispersal initiation dates for philopatric fawns; $n = 77$) and (ii) the movement trajectory scale (using the intensive monitoring sessions occurring once a month on the same date for all individuals monitored in a given year, with one location every 10 min for 24 h, during the three months prior to dispersal). At the movement trajectory scale, these data were available for 49 of the 77 GPS monitored fawns. Three features of the trajectory were estimated: (i) the mean distance between two successive locations; (ii) the mean net square displacement between each location [40] and the barycentre of all locations; and (iii) the mean turning angle between two successive segments and its standard error, providing an index of path sinuosity, with low values corresponding to a more linear path. At the home range scale, only the first two of these metrics were calculated, as path sinuosity with inter-fix intervals of 4 or 6 h is not appropriate [41]. Furthermore, at this scale, the mean distance between two successive locations and the mean distance to the barycentre were strongly dependent on winter home range size. Hence, at the home range scale only, these two metrics were standardized by taking the residuals of the linear regression between the given measure of mobility and the 90% fixed kernel home range estimated between 1st January and 31st March using the 'adehabitat' R package [42] and following Börger *et al.*'s [43] recommendations.

(iii) Head activity

To estimate variation in the level of activity prior to the first dispersal event recorded among fawns, we used the activity sensor data recorded by the GPS collars between the 1st and 28th March. These sensors provide the sum of the number of horizontal and vertical head movements every 5 min. Using the same GPS 3300S collars, Gottardi *et al.* [33] detected high among-individual variability potentially due to variable tightening of the collar around the neck of the animal, so that mean activity could not be compared directly among individuals. To control for this source of variation that is probably not related to actual differences in activity, we centred the values of each sensor for each fawn separately (by subtracting the mean for that individual). Then, variation in head activity among fawns was estimated using the standard deviation of the two variables. High values indicated fawns with high variation in their head movements, i.e. fawns with more strongly contrasted phases of behaviour. In the context of behavioural syndromes, we expected that individuals with more variable head activity (i.e. with a more variable number of up–down and side-to-side head movements) should also be more mobile and more exploratory.

(iv) Stress response

We used body temperature and behaviour at capture to index the reaction of individual deer to a highly stressful event [44]. We assumed that individuals with high body temperature and high behavioural scores had a more acute stress response (note that body temperature may also provide a proxy of individual metabolic rate in non-stressed situations [15]). Since 2009, rectal temperature was measured twice during capture, at the beginning and the end of the handling event (using a Digitemp Color thermometer to the nearest 0.1°C). Each fawn was also assigned a behavioural score based on the occurrence (presence versus absence) or intensity (zero, moderate, strong) of six different behaviours during handling and release: (i) struggle intensity in the net and (ii) on the table during marking, (iii) flight movement type and speed (trotting–moderate, running–moderate, running–high speed) at release, and whether it (iv) fell, (v) staggered or (vi) attempted to remove its collar. The behavioural score was calculated as the mean of these six behavioural items and ranged from zero to one. Behavioural data were available for 52 fawns for which dispersal fates were known, but for four of these, body temperature was not recorded.

(e) Data analysis

To assess how variation among individuals in the four behavioural traits (exploration, mobility, activity and stress response) could translate into a behavioural syndrome, we performed a principal component analysis (PCA) using the 'ade4' R package [45] on the 33 fawns for which GPS, activity sensor and behavioural data were all available. This allowed us to position each fawn along one or more behavioural continuums derived from the covariation among traits (the principal components (PCs)). The number of PCs retained (using the method proposed by Dray [46]) defined the dimensions of the behavioural syndrome. We interpreted an individual's score on the retained PCs as a description of its behavioural type. The PCA included mobility at the home range scale, but not at the movement trajectory scale because of missing values for 20 fawns. The relationships

Table 1. Scores on the first two axes (PC1 and PC2) of the PCA performed on pre-dispersal behavioural measures of roe deer fawns monitored at Aurignac (France), $n = 33$.

behavioural trait	behavioural measure	PC1	PC2
exploration	number of explorations	−0.38	0.85
	total distance travelled during exploration	−0.28	0.92
mobility (home range scale)	mean distance between 2 locations	−0.73	−0.47
	mean distance to the barycentre	−0.83	−0.29
head activity	variability of side–side head movement sequences	−0.58	−0.04
	variability of up–down head movement sequences	−0.36	−0.02
stress response	body temperature at capture	−0.50	0.05
	behavioural score at capture	−0.03	−0.20
eigenvalue		2.15	1.91
variance explained (%)		26.90	23.84

between fawn PC scores and their body mass, sex and landscape sector were tested with simple linear models.

We assessed the relationship between fawn behavioural type (PC scores) and dispersal status with a model selection procedure using the Akaike's information criterion corrected for small sample size (AICc). We controlled for condition- and habitat-dependence in dispersal propensity [27] by including body mass and landscape sector as fixed effects. Potential inter-annual variability in dispersal behaviour was taken into account by including year as a random factor. We thus fitted five candidate generalized linear mixed models (GLMM) for dispersal propensity (dispersal as a binomial response), with or without the scores on the two retained PCs (see Results) using the 'lme4' R package [47]. We retained the model with the lowest AICc value, reflecting the best compromise between precision and accuracy [48]. We also calculated AICc weights as a measure of the likelihood that a given model was the best among the set of fitted models.

As the above analysis was restricted to a subset of the total data collected (i.e. fawns for which data were available for all behavioural traits), we further investigated the effect of the four behavioural traits (based on 11 different measures) on dispersal propensity separately. We fitted separate logistic regressions for dispersal propensity to estimate the explanatory power of each behavioural measure by adding a given measure to the basic model which included body mass and landscape sector as fixed effects and year as a random effect, as above. All statistical analyses were performed with R software v. 2.12.1 [49].

3. Results

Of the 96 fawns with known dispersal fate, 53 were philopatric and 38 dispersed, of which five returned later during summer to their natal area (i.e. pseudo-dispersal events). The overall population dispersal rate was therefore 0.42 ($n = 91$, excluding the pseudo-dispersing individuals). Of the 33 individuals included in the multi-trait analysis, 15 dispersed (including one pseudo-dispersal event), while 18 remained philopatric.

(a) Inter-correlation of behavioural traits

A clear threshold appeared when plotting the proportion of variation in behavioural traits accounted for by the successive PCs, indicating that we should retain only the first two PCs for further analyses [50]. This suggested a behavioural syndrome with two dimensions involving independent combinations of the behavioural traits. These two PCs accounted for 50.7% of the total variation observed among traits (table 1). The first continuum (PC1) described positive covariation among the two measures of mobility, variation in head activity, body temperature and, to a lesser degree, exploration. PC1, thus, distinguished fawns that were mobile, with high body temperature at capture, variable head activity and somewhat exploratory, from fawns that were less mobile, with low body temperature at capture, less variable head activity and somewhat less exploratory (table 1). The second continuum (PC2) described negative covariation of exploration behaviour with mobility, and, to a lesser extent, with the behavioural score during capture (table 1). PC2, thus, distinguished fawns that were more exploratory, but less mobile within their home range and with a less marked behavioural stress response during capture from fawns that were less exploratory, but more mobile and more stressed at capture (table 1). There was a clear negative relationship between PC1 score and body mass (slope of -0.39 ± 0.14, $n = 32$, $r^2 = 0.21$, $F = 8.07$, d.f. $= 30$, $p = 0.008$) and between PC1 score and landscape sector (mean ± s.d.: 1.47 ± 0.95 in the closed sector versus -0.38 ± 1.39 in the open sector, $n = 33$, $F = 9.53$, d.f. $= 30$, $p = 0.004$), while there was no between-sex difference in PC1 score (mean ± s.d.: -0.30 ± 1.29 versus 0.07 ± 1.59 for males and females, respectively, $n = 33$, $F = 0.40$, d.f. $= 30$, $p = 0.73$). PC2 scores were not related to body mass (slope of -0.05 ± 0.14: $n = 32$, $r^2 = 0.0008$, $F = 0.02$, d.f. $= 30$, $p = 0.87$), sex (mean ± s.d.: 0.57 ± 1.53 versus -0.20 ± 1.35 for males and females, respectively, $n = 33$, $F = 1.95$, d.f. $= 30$, $p = 0.17$) or landscape sector (mean ± s.d.: -0.08 ± 0.25 in the closed sector versus 0.32 ± 1.58 in the open sector, $n = 33$, $F = 0.03$, d.f. $= 30$, $p = 0.87$). The relationships between each of the behavioural measures and body mass were, in general, weak ($n = 11$; mean $r^2 = 0.05 \pm 0.05$; min $= 0.002$; max $= 0.14$; electronic supplementary material, appendix S1).

(b) Link between dispersal and behavioural traits

The behavioural continuums identified by the PCA were both linked to subsequent dispersal status, independently of the effects of body mass and landscape sector (figure 1). The best model included the fixed effects of both behavioural continuums in addition to body mass, sector and year (table 2).

Table 2. Model selection for the logistic regressions of dispersal status (disperser/philopatric) in relation to two behavioural continuums corresponding to overall energy budget, PC1 and the degree of neophobia, PC2, body mass and landscape sector for 32 roe deer fawns monitored. The basic model included body mass (BM) and controlled for between-sector and between-year differences by including 'sector' as a fixed effect and 'year' as a random effect. The selected model is given in bold. *k* refers to the number of model parameters.

	k	AICc	ΔAICc	AICcWt
PC1 + PC2 + BM + sector + (1|year)	**6**	**41.74**	**0.00**	**0.83**
PC2 + BM + sector + (1|year)	5	45.20	3.47	0.15
PC1 + BM + sector + (1|year)	5	49.78	8.04	0.01
BM + sector + (1|year)	4	50.38	8.64	0.01

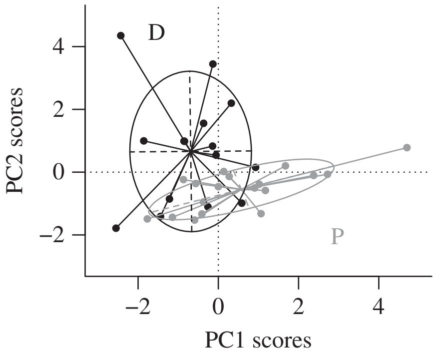

Figure 1. Scatter plot of the 33 roe deer fawns according to their scores on the two PCA axes (PC1 and PC2 scores) representing gradients of energy budget and neophobia, respectively. Future dispersers ('D') are in black and future philopatric roe deer ('P') are in grey.

Philopatric fawns had higher PC1 scores and lower PC2 scores than fawns that dispersed (figure 1).

When analysing the relationship between dispersal propensity and each behavioural measure independently, the models including behavioural score at capture, the number of explorations, the distance travelled during exploration, the distance to the home range centre at the movement trajectory scale and variation in activity of up–down head movements all improved the data fit compared to the basic model (i.e. including body mass and sector as fixed effects and year as a random effect) for predicting dispersal status (table 3). These five behavioural measures were related to dispersal status such that dispersal propensity was greater for fawns that performed more explorations, travelled further during exploration, had lower behavioural scores at capture, had more variable activity of up–down head movements and moved further away from the centre of their home range at the movement trajectory scale (table 3 and figure 2; electronic supplementary material, appendix S2).

4. Discussion

Our work provides, to our knowledge, the first evidence that a multi-trait behavioural syndrome is closely linked with natal dispersal propensity, acting in addition to, and independently of, condition-dependence in a free-ranging population of wild animals. Certain individuals were more likely to disperse than others depending on their pre-dispersal behavioural type composed of two independent behavioural continuums. Moreover, these relationships conformed to our expectations [12,51], as dispersal propensity was greater among individuals that, prior to dispersal, explored more, that were more mobile, with higher variation in head activity, and that exhibited a less marked stress response at capture. Furthermore, since dispersal propensity was linked to the position of an individual along the two independent behavioural continuums while simultaneously accounting for condition-dependence, our results demonstrate that the dispersal decision in this species is governed by a combination of behavioural and morphological traits that together form a dispersal syndrome.

We were able to exploit information from 11 behavioural measures corresponding to four behavioural traits (exploration, mobility, activity and stress response) and so determine individual behavioural types (quantified as an individual's score along the two behavioural continuums) which we could then link to dispersal propensity. The first continuum distinguished fawns with regard to their mobility, variation in head activity, body temperature and, to a lesser degree, exploration propensity, all of which are related to overall energetic balance. Although we had no direct measure of energetic expenditure, this continuum probably reflects among-individual variation in the overall level of energy budget, with negative scores indicating fawns with energetically costly behaviours devoted, for example, to exploration or mobility. Indeed, active fawns have a higher metabolic rate [15,52], as do more exploratory individuals [53]. Body temperature at capture reflects the combination of two physiological components: in a non-stressed situation, body temperature is a proxy of individual metabolic rate [15], while in a situation of stress, body temperature rises and indicates 'stress-induced hyperthermia' [54,55]. Here, we interpret body temperature at capture to reflect the effects of among-individual differences in metabolic rate modulated by the stress response. Our interpretation is supported by the fact that this behavioural continuum was positively related to individual body mass, as a positive correlation between metabolic rate and body mass is commonly reported [56], while several studies have also found a positive relationship between metabolic rate and behavioural traits such as activity, aggressiveness, exploration or boldness [57]. We found that dispersal propensity was related to an individual's score along this behavioural continuum of overall energetic budget, indicating that the decision to disperse is linked to physiological status. This is in agreement with earlier observations of a strong link between dispersal propensity and body mass in the same study population [27]. Dispersal is presumed to be costly [58], hence larger fawns with high overall energetic expenditure are likely to be better able to afford these potential costs than lighter individuals with low energy budgets. Hence, we suggest that the link between dispersal propensity, body mass and the energetic budget continuum is related to dispersal costs, and

Table 3. Effects (slope ± s.e.) of behavioural traits on dispersal propensity of roe deer fawns monitored at Aurignac (France). The basic model included the fixed effects of body mass and landscape sector and the random effect of year. ΔAICcBasic refers to the difference in AICc between the model with and without the given behavioural measure; a negative value of ΔAICcBasic means that the model including the behavioural measure explains dispersal propensity better than the basic model; *n* refers to the number of individuals used, *k* to the number of model parameters. HR, home range scale; mvt, movement trajectory scale.

behavioural trait and measure		*n*	*k*	ΔAICcBasic	AICcWt	slope ± s.e.	standardized slope ± s.e.
exploration	number of explorations	76	5	−7.06	0.97	0.84 ± 0.32	0.06 ± 0.02
	total distance travelled during exploration	76	5	−1.12	0.64	0.0001 ± 0.00005	0.04 ± 0.02
mobility_HR	mean distance between 2 locations	76	5	1.64	0.31	0.004 ± 0.005	0.003 ± 0.007
	mean distance to the barycentre	76	5	1.28	0.35	−0.51 ± 0.52	−0.007 ± 0.005
mobility_mvt	mean distance between 2 locations	47	5	1.10	0.37	0.04 ± 0.03	0.03 ± 0.02
	mean distance to the barycentre	47	5	−2.02	0.73	0.68 ± 0.36	0.09 ± 0.05
	index of path tortuosity	47	5	1.58	0.31	−3.41 ± 3.52	−0.08 ± 0.08
head activity	variability of side–side head movement sequences	70	5	2.33	0.24	0.17 ± 4.758	0.02 ± 0.05
	variability of up–down head movement sequences	70	5	−2.32	0.76	20.02 ± 9.77	0.14 ± 0.09
stress response	body temperature	49	5	2.41	0.23	−0.16 ± 0.52	−0.08 ± 0.21
	behavioural score	51	5	−0.71	0.59	−3.33 ± 1.98	−0.03 ± 0.02

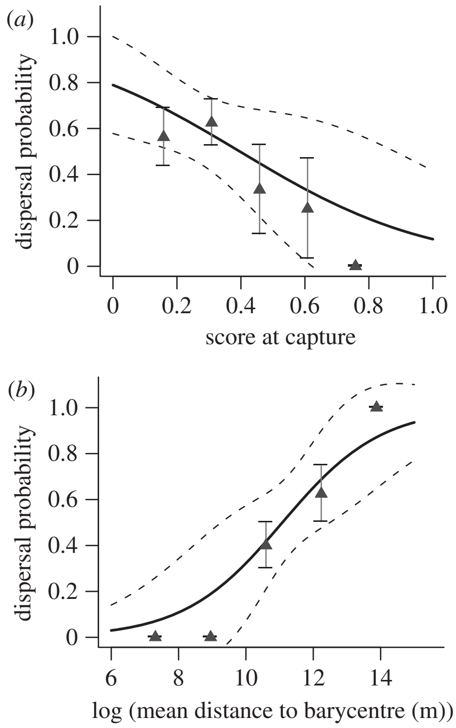

Figure 2. Relationship of dispersal propensity with (*a*) behavioural score at capture and (*b*) mean distance to the barycentre at the movement scale, while controlling for variation in body mass and landscape sector (as a fixed effect, and with the open sector taken as a reference) and including the year of monitoring as a random factor ($n = 51$ and 47, respectively). Dashed lines represent the 95% CIs around the predicted values, and grey triangles represent the observed probability of dispersing with its standard error.

consequently that natal dispersal is voluntary rather than enforced in roe deer. These results are in agreement with previous studies reporting that future dispersers were faster explorers than locally born individuals (in great tits [17]) or that exploration distance and orientation predicts dispersal features (in red squirrel *Tamiasciurus hudsonicus* [59]).

The second behavioural continuum distinguished fawns that avoided new situations (low exploration distances), were mobile within their home range (i.e. within a known environmental context) and, to a lesser degree, reacted strongly to a stressful and novel situation (the capture event) from fawns that explored more widely, were less stressed at capture, but were less mobile within their home range. We, thus, interpret this continuum as a gradient of neophobia such that high scores characterize fawns that have a fear of novelty, exhibiting no exploratory behaviour, but that can be highly mobile inside their home range, and react strongly during the capture event. Neophobia is commonly defined as an aversion to unfamiliar conditions [60], and individuals that avoid novel situations and are stressed when confronted with a novel event can thus be described as neophobic. Inter-individual variation in the degree of neophobia has been found in a variety of bird species [61,62]. Neophobia may be driven by selection pressure for predator and/or risk avoidance [63]. Variation in the response of individuals to capture (body temperature and breathing rate) was found to be a reliable indicator of acute stress in great tits and was also related to the shy–bold continuum [44]. As boldness is linked to the propensity for an individual to take risks [64], our neophobia score could thus also be interpreted as a proxy of boldness. In this case, as we found that dispersal propensity was higher among roe deer fawns with low neophobia, this would suggest that dispersal is more common among bold individuals. The bold–shy continuum is a well-studied component of animal personality and boldness has previously been linked to animal movements. For example, boldness was positively linked to migratory propensity in roach *Rutilus rutilus* [65], to intermittent locomotion in juvenile bluegill sunfish *Lepomis macrochirus*, with bolder individuals moving more often and faster [66], and to exploratory behaviour in male great tits [67]. However, evidence for a link between boldness and dispersal propensity remains scarce (but see [16] for a relationship with dispersal distance in the Trinidad killifish).

In our population, we found clear evidence for a link of dispersal propensity with four independent behavioural traits, that is, exploration, activity, mobility and stress response, as well as with individual condition (mass) (table 3). Moreover, by considering covariation among these traits, we were able to show that dispersing fawns had higher energetic budgets and less neophobic behaviour compared with philopatric fawns. However, identification of behavioural syndromes (or personalities) generally requires that individuals are measured more than once for a given trait [13]. Although we were unable to obtain repeated measures of the behavioural traits in our case study of a free-ranging roe deer population, exploration, mobility and activity were all estimated from field data covering a considerable period of time (continuous GPS monitoring over several weeks) during which individuals were likely to be confronted with a variety of different contexts [62]. Thus, while we cannot definitively conclude that the link we identified between dispersal propensity and behavioural type is the expression of individual personalities, we clearly showed that dispersal is likely to be personality-dependent in roe deer.

In this study, we demonstrated additive associations of both behavioural and morphological traits for explaining dispersal propensity, suggesting the existence of one or more dispersal syndromes in this large mammal, such that individuals with high overall energetic budgets and/or low levels of neophobia and/or high body mass were more likely to disperse. This result highlights the importance of using a multi-trait approach and suggests that associations of suites of behavioural and morphological traits with dispersal outcomes could be widespread. However, multi-trait dispersal syndromes have rarely been investigated, although dispersal outcomes in the common lizard appear to depend on the interaction between social (i.e. sociality) and environmental (i.e. density) contexts [19]. It would be intriguing to extend this type of approach in other systems in order to explore whether such multiple associations between behavioural traits and dispersal generally occur for a given condition. Indeed, it appears that different ecological and social contexts can drive the dispersal decision and thus explain the association of different behavioural types with dispersal outcomes [12].

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Data accessibility. Data on dispersal behaviour and behavioural traits have been uploaded as the electronic supplementary material.

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