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# Sex differences in condition dependence of natal dispersal in a large herbivore: dispersal propensity and distance are decoupled

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Evolution should favour plasticity in dispersal decisions in response to spatial heterogeneity in social and environmental contexts. Sex differences in individual optimization of dispersal decisions are poorly documented in mammals, because species where both sexes commonly disperse are rare. To elucidate the sex-specific drivers governing dispersal, we investigated sex differences in condition dependence in the propensity and distance of natal dispersal in one such species, the roe deer, using fine-scale monitoring of 146 GPS-collared juveniles in an intensively monitored population in southwest France. Dispersal propensity increased with body mass in males such that 36% of light individuals dispersed, whereas 62% of heavy individuals did so, but there was no evidence for condition dependence in dispersal propensity among females. By contrast, dispersal distance increased with body mass at a similar rate in both sexes such that heavy dispersers travelled around twice as far as light dispersers. Sex differences in the strength of condition-dependent dispersal may result from different selection pressures acting on the behaviour of males and females. We suggest that females disperse prior to habitat saturation being reached, likely in relation to the risk of inbreeding. By contrast, natal dispersal in males is likely governed by competitive exclusion through male–male competition for breeding opportunities in this strongly territorial mammal. Our study is, to our knowledge, a first demonstration that condition dependence in dispersal propensity and dispersal distance may be decoupled, indicating contrasting selection pressures drive the behavioural decisions of whether or not to leave the natal range, and where to settle.

## 1. Introduction

Natal dispersal, the movement away from the natal site to the site of first reproduction, is a crucial life-history trait that influences gene flow, metapopulation dynamics and, ultimately, the spatial distribution of species [1,2]. Furthermore, dispersal is a key component of a species' response to global change [3], facilitating shifts in geographic range in response to rapid and wide-scale modifications of suitable environmental conditions [4]. Dispersal is driven by inbreeding avoidance, resource competition, particularly among kin and habitat heterogeneity [1,5]. However, the dispersal decisions an individual takes depend on the predicted cost-benefit balance of dispersal in relation to that individual's phenotype and current condition, or state. Hence, in a given environmental context, the behavioural responses of individuals within a population that ultimately result in dispersal, should differ (condition-dependent dispersal *sensu* [6]). Condition dependence occurs when dispersal behaviour is influenced by any internal state variable [7,8], for example, an individual's sex [9], age [10] or body condition [11,12].

There has been much research over the last three decades focusing on why dispersal is generally more prevalent in one sex or the other in a given species [9,13]. For example, dispersal is male biased in most mammals [14–16], whereas it is generally female biased in birds [17,18]. This difference is potentially linked to differences in mating tactic, social environment, sexual size dimorphism or asymmetry in parental care [9,16,19]. In polygynous species, females are generally limited by scramble competition for resources to offset the costs of reproduction [20]. Hence, dispersal is expected to be voluntary and to increase as a function of local density so that females should approximate an ideal free distribution (*sensu* [21]). According to the habitat saturation hypothesis, dispersal propensity should peak when the carrying capacity of the habitat has been reached, so that only those individuals that may benefit from the death of a conspecific are philopatric [22]. By contrast, because polygynous males are limited by breeding opportunities in terms of access to females through male-male contest competition [20], dispersal is expected to be enforced, resulting from competitive exclusion by dominant individuals [23]. This dichotomy in life-history constraints between the sexes should drive the evolution of divergent sex-specific dispersal tactics [24,25].

Given that dispersal is costly ([26], for a case study see [27]), individuals are expected to optimize their dispersal tactics (individual optimization *sensu* [28]) in relation to the total amount of energy available to them, and their overall strategy of allocation to competing biological functions. Individual optimization of dispersal decisions is expected to differ between the sexes because polygynous males must also allocate energy to sexually selected traits such as body growth and secondary sexual characters (e.g. antlers). While relatively rare [29], species where both sexes commonly disperse provide ideal model systems to identify sex-specific drivers governing condition-dependent dispersal decisions (e.g. [30,31]). One such species is the roe deer, which is widely distributed across Europe and has been intensively studied over much of its range [32], especially with regard to natal dispersal (e.g. [33,34]). Recent studies have indicated that natal dispersal of roe deer is equally prevalent in both sexes [35,36], does not fluctuate with population density [36] and increases with body condition [37,38], but the sex-specific nature of this relationship remains poorly

understood. Earlier work suggested that the proximate mechanism driving male dispersal is male-male competition for access to a mating territory [34]. Resident territorial males direct most of their aggressive interactions towards the most sexually mature juveniles with larger than average antlers [34], which are also heavier [39], presumably because these individuals pose the most threat in terms of territory loss. By contrast, female roe deer are not territorial and were initially reported to be distributed according to an ideal free distribution [40], although subsequent investigations did not support this [41]. Gaillard *et al.* [36] found no direct relationship between density and either dispersal propensity or dispersal distance at the population level. These findings indicate that the habitat saturation hypothesis does not satisfactorily account for patterns of dispersal in roe deer. Instead, as in brown bears [42], dispersal in roe deer might peak during the pre-saturation phase, prior to the carrying capacity of the habitat being reached (*sensu* [22]). Under this scenario, individual females, whose reproductive success is more tightly linked to food resources than that of males, should optimize their dispersal decisions in relation to the spatial distribution of resources.

In order to understand better the sex-specific drivers of natal dispersal, we analysed sex differences in condition-dependent natal dispersal in an intensively monitored population of European roe deer. We focused on body mass, a common measure of phenotypic quality [43] that decreases with increasing density-dependent competition for resources [44]. Following Wahlström [34], we expected positive condition dependence in dispersal propensity of males such that heavier individuals are more likely to disperse in response to increased competition with adult males. However, when dispersal is voluntary, *motivation* to disperse is predicted to be low when density-dependent competition is locally low because individuals can achieve higher body condition [45]. As density increases so that average body condition decreases, the *capacity* to disperse should be limited by energetic constraints. Hence, we expected female dispersal to be most frequent at intermediate values of body mass, before scramble competition for resources is severe enough to limit body growth so that the body mass threshold necessary for successful dispersal cannot be reached [37]. Finally, sexual size dimorphism of roe deer is rather weak (adult males weigh only 10% more than females, [46]) so that dispersal is likely equally energetically costly for both sexes [47]. Because heavier animals are in better condition in an income breeder such as roe deer [48], they should be better able to cope with the costs of dispersal and, thus, can afford to travel further to locate a high-quality range [26]. Hence, we expected dispersal distance to increase with body mass and in a similar manner for both sexes.

## 2. Material and methods

### (a) Study system

We quantified natal dispersal of 146 GPS monitored juvenile roe deer (68 males, 78 females) in an intensively monitored population in Val-lons et Coteaux de Gascogne (Zone Atelier PyGar), southwest France (N 43°17', E 0°53'). It is a low elevation (260–380 m.a.s.l.), mixed-use agricultural landscape (19 000 ha) composed of remnant woodland patches (18.8%), hedgerows (3.6%), meadows (37.2%) and arable land (31.6%), with scattered villages. Roe deer density was estimated using a capture-mark-resighting approach to average around eight individuals per 100 ha in the mixed open landscape.

No natural predators of adult deer were present, although stray dogs occasionally killed both fawns and adults. Hunting mostly occurred during winter, although some males were also hunted during summer. Around 15% (*ca* 130 individuals) of the population is removed by hunting each year (unpublished data from the Hunting Regional Agency).

### (b) Capture and monitoring

Deer were caught from 2004 to 2017 during winter (November–March), several months prior to the dispersal season in this species, using drive netting. Juveniles were identified based on the presence of a tri-cuspid milk premolar tooth ( $P_3$ , which is replaced between 10 and 15 months of age, [49]), sexed and weighed (to the nearest 0.1 kg) with an electronic balance. Deer were equipped with a GPS collar (Lotek or Vectronic Aerospace) which recorded their location at 6 h intervals year-round, before being released on site. We removed all GPS fixes taken during the first 8 days after capture because of the potential disruption of normal spatial behaviour due to capture [50], and GPS fixes for which the location was obviously erroneous (0.0003% of the location dataset) as they implied an unfeasible movement speed.

All capture and marking procedures were approved by the local authority for animal welfare (Departmental Authority of Population Protection, agreement no. A31113001).

### (c) Measuring dispersal

We measured natal dispersal during each animal's second spring/summer with two metrics, dispersal propensity and dispersal distance. In the vast majority of cases, natal dispersal of roe deer occurs only once in an individual's lifetime, during the animal's second spring/summer at around 10–15 months of age, and involves a clearly defined movement, or transience, from the natal area to a new post-dispersal home range, which is then occupied for the rest of the individual's lifetime [33,37]. Because roe deer juveniles remain strongly associated with their mothers during their first year of life, and because adult females are highly sedentary [32], we assumed that the observed winter range was strictly equivalent to the pre-dispersal natal range. Based on stability in space use, exploration events and directionality of movement, we recently classified all monitored juveniles from this population into one of six categories [51]: classic dispersers (with a clearly defined transience movement between spatially distinct pre- and post-dispersal ranges), aborted dispersers (dispersers that returned, on average, 84.8 days later to their natal range,) progressive dispersers (dispersers with a less well-defined transience stage), explorer philopatric (philopatric individuals that performed occasional short-term exploration events outside their home range), multi-rangers (philopatric individuals with several sequentially occupied sub-ranges) or strict philopatric individuals (see fig. A2 in [51] for individual plots of all movement trajectories). Here, because we were interested in condition dependence of the decision to emigrate, we used a simple binary definition of disperser (i.e. pooling classic, aborted and progressive dispersers) versus philopatric (i.e. pooling explorer, multi-range and strict philopatric individuals) based on the above classification to measure dispersal propensity. Then, to measure dispersal distance (dispersers only), we first discarded all locations during the transience phase, defined as the movement trajectory linking the pre- and post-dispersal home ranges. Dispersal distance was then quantified as the distance between the geometric centres of all GPS locations within the pre-dispersal and the post-dispersal ranges.

### (d) Standardizing body mass to 1 February

The body mass of juvenile roe deer may fluctuate over their first winter in relation to the onset and duration of winter [52].

Therefore, we first corrected for over-winter changes in body mass by fitting a simple linear regression model to body mass values in relation to Julian date (24 November JD=0; 5 March JD=101). Because, on average, males weigh slightly more than females [46], we included sex as an additive effect in this model. We then used the regression coefficient of the common slope to standardize individual body mass by date for both sexes (i.e. conserving sexual size dimorphism), expressed as the predicted body mass on 1 February (JD = 32, approx. median date of capture).

### (e) Dispersal propensity

We fitted a generalized linear model (GLM) to assess the relationship between dispersal propensity (binomial response variable: 1 the animal dispersed, 0 the animal remained philopatric, all years pooled) and individual body mass on 1 February, while accounting for sex differences in this relationship. Because we expected the strength of condition dependence in dispersal propensity to differ between sexes, we also included the two-way interaction between body mass on 1 February and sex in the most complex model. We then performed model selection using AICc to identify the model that best fit the data [53]. We interpreted the effects contained in the competing models in relation to their respective AICc weights, which provide a measure of the relative likelihood that, among all models fitted, a given model best explains the data. Finally, given that model selection indicated support for a sex-specific relationship between dispersal propensity and body mass (see Results), we then investigated whether this relationship was better described by a linear, quadratic or threshold (using the 'chngpt' library in R) model for each sex separately.

### (f) Dispersal distance

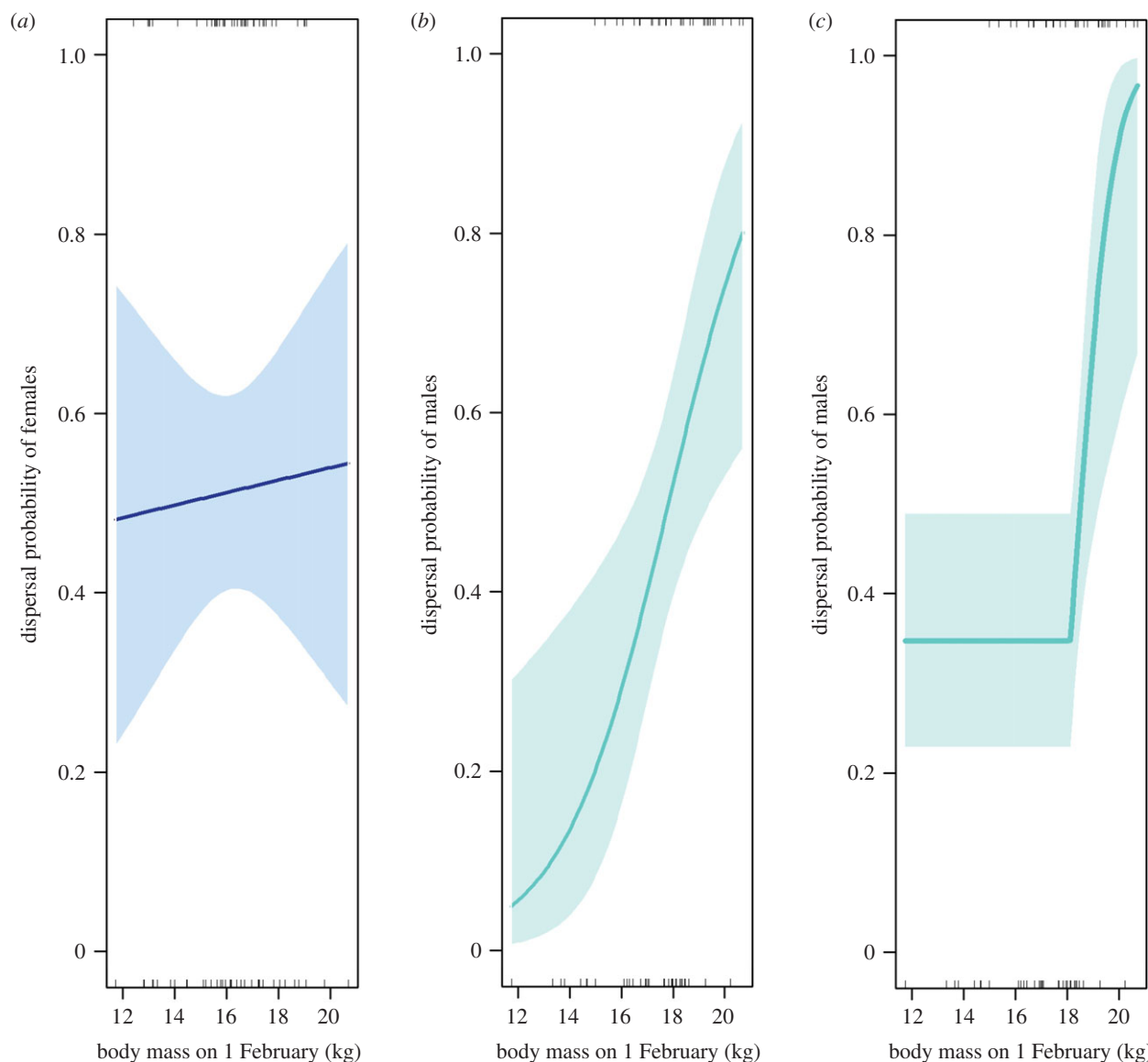
We analysed condition dependence of dispersal distance on the sub-set of individuals that dispersed (i.e. classic, aborted and progressive dispersers). Because the variance of dispersal distance should increase with its mean, to control for heteroscedasticity, we used a linear model with a generalized least-squares (GLS) modelling framework [54] to model dispersal distance as a function of individual body mass on 1 February and sex. A GLS approach allows incorporating weights to control for heteroscedasticity, assuming that variance increases as a power function of the absolute fitted values of dispersal distance (weights = varPower, [54]). We included the two-way interaction between body mass and sex, and used the same model selection procedure based on AICc.

All generalized models were fitted using the 'glm' function in the 'stats' library implemented in R software, version 3.6.1 [55]. All generalized least-squares models were fitted using the 'gls' function in the 'nlme' library [56]. We used the 'dredge' function in the MuMIn library [57] to generate the set of candidate models that we defined *a priori* based on our biological hypotheses (see above).

## 3. Results

### (a) Dispersal propensity

The model containing the main effect of sex only was not competitive compared to the null model ( $\Delta\text{AICc} = 1.79$ , electronic supplementary material, table S1), indicating that there was no overall difference in dispersal propensity between males and females. Dispersal propensity averaged 49.3% over the whole sample (females:  $N = 35/68$ , 51.5%; males:  $37/78$ , 47.1%). However, the best model explaining observed variation in dispersal propensity included a sex-specific effect of body mass on 1 February and, based on AICc weights, was about three times as likely to adequately describe the data as the



**Figure 1.** Dispersal propensity in relation to body mass on 1 February for male and female juveniles in the Aurignac roe deer population ( $N = 146$ ). (a,b) The predicted sex-specific relationships derived from the best GLM model, which included the interactive effects of sex and body mass. (c) The predicted relationship for males only based on a threshold model (threshold at 18.1 kg, see text for details). (Online version in colour.)

second-best model ( $\Delta\text{AICc} = 2.36$ ), which included the simple effect of body mass only (electronic supplementary material, table S1). In males, dispersal propensity increased markedly with increasing body mass so that dispersal propensity increased more than eightfold (from less than 10% to around 80%) over the recorded range of body mass (figure 1, table 1 for parameter estimates). A threshold model of this relationship indicated some support for a breakpoint at around 18 kg (maximal statistic = 11.4, threshold = 18.1,  $p$ -value = 0.003) such that dispersal propensity averaged around 36% among individuals below this threshold, but 62% above it. By contrast, dispersal propensity in females was approximately constant irrespective of body mass (figure 1) such that heavy females dispersed with approximately the same probability as lighter females. This was the case irrespective of whether body mass was included as, alternatively, either a linear, a quadratic or a threshold function ( $\Delta\text{AICc}$  with the null model greater than 2).

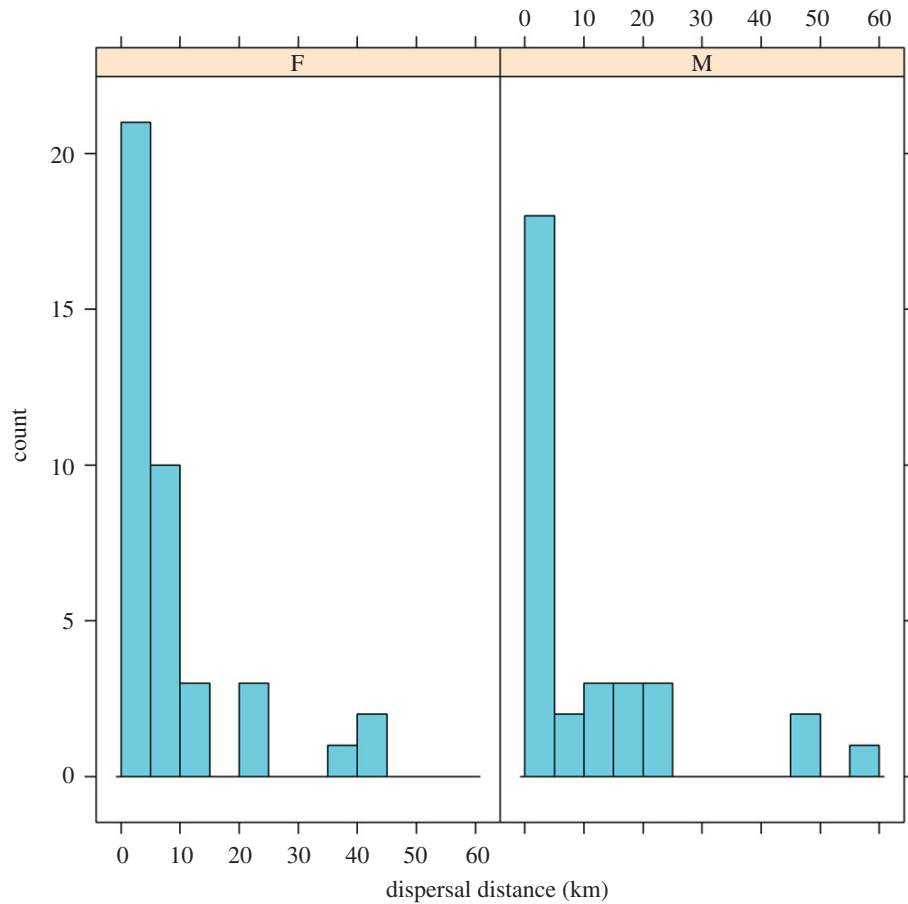
### (b) Dispersal distance

Dispersers travelled an average of 9.6 km (males: mean = 11.1 km, median = 3.6 km; females: mean = 8.4 km, median =

4.4 km), ranging between a minimum of 0.3 and a maximum of 56.4 km (figure 2). The best model explaining observed variation in dispersal distance included an effect of body mass on 1 February only, and was about three times as likely to adequately describe the data as the second-best model ( $\Delta\text{AICc} = 2.12$ ), which included the additive effects of body mass and sex (electronic supplementary material, table S2). Dispersal distance increased with body mass in both sexes (figure 3, table 1), and this increase was of a similar magnitude in males and females (estimated difference in slope of  $0.66 \pm \text{s.d. } 1.60 \text{ km kg}^{-1}$ ,  $p = 0.68$ ). Heavy (greater than 16 kg, males and females combined) dispersers travelled around twice as far as light (less than 16 kg) dispersers (mean  $\pm$  s.d.: light =  $5.3 \pm 9.5$  km, range: 0.4–43.1 km; heavy =  $11.3 \pm 13.8$  km, range: 0.3–56.4 km), irrespective of their sex.

## 4. Discussion

Individual optimization of dispersal tactics is expected to differ between the sexes because the costs and benefits of avoiding inbreeding or resource competition are likely to be

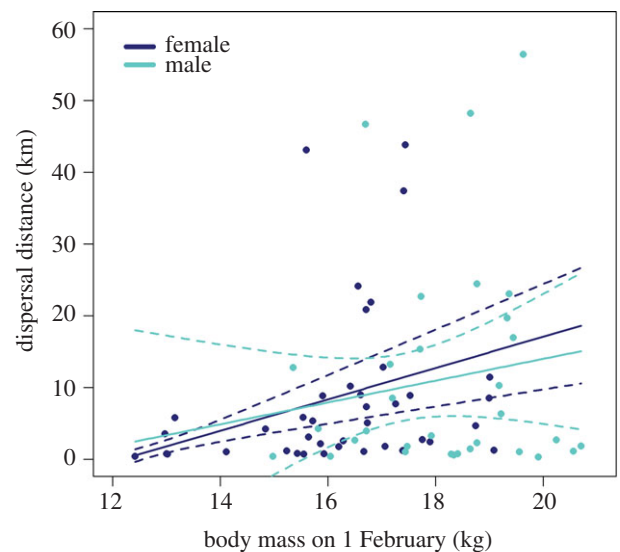


**Figure 2.** Dispersal distance kernels (km) for dispersing male and female juveniles in the Aurignac roe deer population ( $N = 72$ ). (Online version in colour.)

**Table 1.** Parameter estimates with standard errors and z-values for the retained models describing a. variation in dispersal propensity (on a logit scale) in relation to body mass on 1 February and sex, and the two-way interaction between body mass and sex; and b. variation in dispersal distance (km) in relation to body mass on 1 February. For the sex term, the reference category is female.

response variable	parameter	estimate $\pm$ s.e.	z-value
a. dispersal propensity	(intercept)	$-0.40 \pm 1.98$	-0.202
	sex (male)	$-8.25 \pm 3.70$	-2.231
	body mass	$0.03 \pm 0.12$	0.230
	sex (male) $\times$ body mass	$0.46 \pm 0.21$	2.138
b. dispersal distance	(intercept)	$-24.121 \pm 4.947$	-4.875
	body mass	$1.995 \pm 0.371$	5.376

sex-specific [58]. Species of mammals in which natal dispersal is equally prevalent in both sexes are rare [29], but provide excellent models to test key hypotheses on sex differences in the evolution of dispersal. Here, we analysed natal dispersal of one such species, the roe deer, and found contrasting patterns of condition dependence between the sexes in dispersal propensity, but not dispersal distance. As expected, both dispersal propensity and distance consistently increased with increasing body mass in males. By contrast, females emigrated from their natal range irrespective of their body mass, but among those that did disperse, heavier individuals



**Figure 3.** Dispersal distance (km) in relation to body mass on 1 February for dispersing male and female juveniles in the Aurignac roe deer population ( $N = 72$ ). The data points and respective best-fit lines are indicated in light shading for males and dark shading for females for visualization purposes only. The selected model indicated that there was no sex difference in the slope of the relationship between dispersal distance and body mass, but that the common slope differed from zero (see Results and electronic supplementary material, table S2). (Online version in colour.)

travelled farther. We suggest that this sex-specific pattern is due to different selection pressures acting on dispersal behaviour of males and females [25,58]. We thus provide one of the first demonstrations that condition dependence

in dispersal propensity and dispersal distance may be decoupled, indicating that the decisions of whether (or not) to leave the natal range and where to settle are driven by different behavioural mechanisms.

### (a) Dispersal and local resource competition in females

Emigration has been frequently observed to increase with resource competition [5,59,60]. Body mass of juveniles during their first winter is a highly informative metric of resource limitation in large herbivores in general [61] and in roe deer in particular [48]. Therefore, heavy juveniles likely experienced low levels of scramble competition for resources, whereas light juveniles experienced resource limitation during early life. Furthermore, at the individual level, body mass during the first winter is a reliable proxy of individual quality in both sexes [43]. We expected female dispersal to be most prevalent at intermediate values of body mass, when both motivation (driven by declining habitat quality) and capacity (driven by individual body condition) are high (see [45]), before scramble competition for resources is severe enough to limit body growth. However, we found no support for this hypothesis, as around half of all females dispersed, irrespective of their body mass (figure 1). We suggest that female roe deer disperse independently of habitat saturation and, as a result, irrespectively of population density [36]. Instead, the dispersal of female roe deer is driven by the spatial distribution of resources and is expected to be context-specific rather than individual-specific. In the studied population with a rich and stable resource distribution, about half of all female juveniles dispersed well before habitat saturation, generating a pattern of pre-saturation dispersal similar to that previously reported for brown bears [42]. This is likely the prevailing situation in human-dominated landscapes, where hunting, car collisions and mowing limit population growth rate, while agricultural crops provide high-quality resources, ensuring rapid body development and excellent fitness prospects [62].

Although we found no evidence for body condition-dependent *dispersal propensity* of female juveniles, we did find strong evidence for body condition-dependent *dispersal distance* (figure 3). That is, among the 50% of individuals that dispersed, heavy females travelled, on average, about 73% further than relatively light females (average dispersal distance =  $12.2 \pm 2.2$  km for a female juvenile that was 2 kg heavier than average, compared to  $7.0 \pm 2.2$  km for a female that was 2 kg lighter than average). This suggests that if females in good condition do disperse, on average, they travel further across the landscape because they can afford to be more selective in order to locate a high-quality range. Indeed, dispersing females should preferentially settle in habitat patches of high quality and with low levels of competition [63], potentially using similarity with the natal range as a cue for identifying a suitable habitat patch (natal habitat preference induction, *sensu* [64]). Successful settlement has been shown to depend on body condition, with larger or heavier individuals successfully accessing already populated habitat in lizards [65] or habitat patches of higher quality in great tits [66].

While we hypothesize that the relationship that we reported between body mass and *dispersal distance* could be driven by spatial variation in resource distribution, in the light of our results, we suggest that resource competition may not be the primary factor behind the decision whether

to leave the natal range. Instead, we suggest that female roe deer initiate dispersal in relation to the risk of breeding with a strongly related partner. This risk is potentially substantial due to very high site fidelity of both sexes over their reproductive lifespan, together with a strongly territorial mating system [67]. Given that around 50% of juveniles are philopatric (our results), this creates opportunities for incestuous mating between mother and son or father and daughter. Indeed, inbreeding avoidance is predicted to be a powerful selective force promoting dispersal in a wide variety of organisms [68]. This might be the case in roe deer as around half of all sexually mature females perform breeding excursions outside their usual range during the rut, presumably to reproduce with an unrelated partner [69]. Indeed, by coupling kin recognition with mate choice, females can avoid inbreeding without incurring some of the costs linked to true dispersal (see [31] for a similar argument in male African wild dog).

### (b) High-quality males have to leave: competitive exclusion and local mate competition

The social dominance hypothesis predicts that weaker or subordinate individuals will be evicted by more dominant individuals when the local competition is strong [11,70]. Wahlström [34] suggested that territorial males may aggressively target particularly well-developed juveniles to avoid future competition for mating territories. Our findings are in line with this hypothesis [71] as *dispersal propensity* consistently increased with body mass in male juveniles. By contrast, Loe *et al.* [72,73] reported that dispersal propensity in male red deer decreased as density increased, but was not related to individual body mass. This between-species difference might be linked to the lower frequency of agonistic interactions and higher costs of emigrating from the matriarchal group in the non-territorial, but highly polygynous red deer male compared to the highly territorial male roe deer.

Gyllenberg *et al.* [70] demonstrated that dispersal of competitively strong individuals may be a common outcome under kin competition (e.g. [30] for a case study). In territorial species, the social fence hypothesis assumes that dispersers have to be large to win agonistic interactions with residents in order to settle in a new territory (e.g. [74]). Roe deer males are strongly territorial from March to September, defending a mating territory concomitantly with the entire period when juveniles disperse and settle [67]. The positive relationship we reported between *dispersal propensity* and body mass supports the interpretation that competition for future access to a mating territory between high-quality juveniles and resident bucks is the main driver behind dispersal of males. However, *dispersal distance* in male juveniles increased markedly with body mass in much the same way as in females, with most males dispersing just a few kilometres away from their natal range. These results are coherent with the hypothesis that dispersal of heavy juvenile males is driven by competitive exclusion [23], with males dispersing until they locate the nearest vacant territory that will provide access to reproductive females [67].

### (c) Individual quality and the cost of dispersal

Individuals should optimize dispersal decisions in relation to both condition-dependent competitive ability and costs [70]. Our data indicate that both *dispersal propensity*, at least for

males, and *dispersal distance* were low in light juveniles, whereas long-distance dispersal was observed almost exclusively in heavier than average individuals (only one lighter than average individual of each sex dispersed further than 15 km). This indicates that dispersal is costly and that only the most robust individuals are able to cope with the costs of long-distance dispersal. In support of this, we recently showed that, during transience, dispersers travel 63% further per day and expend 22% more energy compared to philopatric individuals [75]. During both transience and settlement, dispersers are also likely to suffer missed feeding opportunities [75] and greater stress [27], likely generating substantial life-history costs (e.g. [76]). In agreement, Johnson *et al.* [77] found that mortality risk increased with dispersal distance in juvenile American martens (*Martes americana*) so that individuals in poor condition settled closer to their natal range. Indeed, poor condition individuals may be forced to be less selective with regard to habitat quality in the settlement range so as to limit dispersal costs [78]. For example, owls in poor condition dispersed along straighter paths than owls in good condition, likely in relation to the costs of searching for suitable habitat [79]. Opportunity costs (*sensu* [26]) for dispersers due to loss of familiarity with the environment may, indeed, be substantial [80].

## 5. Conclusion

Our findings demonstrate that while the ultimate drivers generate a similar overall level of dispersal in the two sexes, a given average propensity to disperse hides a strongly sex-specific pattern of dispersal linked to contrasting mechanisms of individual optimization in males and females. Moreover, while propensity to disperse and dispersal distance are often viewed as two alternative metrics for measuring the strength of dispersal, our study demonstrates that they rather correspond to two sequential components of the dispersal process, which are subject to different selection pressures. We found that dispersal in roe deer is a state-dependent process (*sensu* [81]) whereby an individual makes decisions with adaptive consequences based on its condition. Body mass attained

prior to dispersal predicts survival and adult mass [82] and is thereby a reliable indicator of phenotypic quality. About one in two females dispersed, irrespective of quality, potentially motivated by the local risk of inbreeding. When they did disperse, females of high phenotypic quality appeared able to afford the costs of travelling farther from their natal site to locate a suitable home range. However, individual optimization in dispersal behaviour of males involved different cues, as both propensity to disperse and dispersal distance increased with increasing phenotypic quality. The similarity in the sex-specific patterns of dispersal distance seems to be a direct reflection of dispersal costs, with higher quality individuals better able to meet the high energy requirements of long-distance dispersal (see [75]), irrespective of their sex. By contrast, the marked difference in the shape of condition dependence in dispersal propensity indicates that males and females respond to different drivers when taking the decision whether or not to disperse. Future research will be required to assess whether individuals that best track the population-level decision rule, given their phenotypic quality, gain fitness benefits compared to individuals that deviate from the average sex-specific trajectory.

**Data accessibility.** All raw data are stored in the EURODEER spatial database hosted by the Fondazione Edmund Mach (<https://euromammals.org>) and can be accessed upon login. The sub-set of the data used in the current analysis are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.nvx0k6drh> [83].

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**Competing interests.** We declare that we have no competing interests.

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## References

- Clobert J, Baguette M, Benton TG, Bullock JM. 2012 *Dispersal ecology and evolution*. Oxford, NY: Oxford University Press.
- Ronce O. 2007 How does it feel to be like a rolling stone? Ten questions about dispersal evolution. *Annu. Rev. Ecol. Evol. Syst.* **38**, 231–253. (doi:10.1146/annurev.ecolsys.38.091206.095611)
- Berg MP, Kiers E, Driessen G, Van Der Heijden M, Kooi BW, Kuenen F, Liefing M, Verhoef HA, Ellers J. 2010 Adapt or disperse: understanding species persistence in a changing world. *Glob. Change Biol.* **16**, 587–598. (doi:10.1111/j.1365-2486.2009.02014.x)
- Parmesan C *et al.* 1999 Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature* **399**, 579–583. (doi:10.1038/21181)
- Bowler DE, Benton TG. 2005 Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. *Biol. Rev.* **80**, 205–225. (doi:10.1017/S1464793104006645)
- Ims RA, Hjermann DO. 2001 Condition-dependent dispersal. In *Dispersal* (eds J Clobert, EDanchin, AA Dhondt, JD Nicos), pp. 203–216. New York, NY: Oxford University Press.
- Dufty AM, Belthoff JR. 2001 Proximate mechanisms of natal dispersal: the role of body condition and hormones. In *Dispersal* (eds J Clobert, E Danchin, AA Dhondt, JD Nicos), pp. 217–229. New York, NY: Oxford University Press.
- Massot M, Clobert J, Lorenzon P, Rossi JM. 2002 Condition-dependent dispersal and ontogeny of the dispersal behaviour: an experimental approach. *J. Anim. Ecol.* **71**, 253–261. (doi:10.1046/j.1365-2656.2002.00592.x)
- Trochet A, Courtois EA, Stevens VM, Baguette M, Chaine A, Schmeller DS, Clobert J, Wiens JJ. 2016 Evolution of sex-biased dispersal. *Q. Rev. Biol.* **91**, 297–320. (doi:10.1086/688097)
- Ekman J, Griesser M. 2002 Why offspring delay dispersal: experimental evidence for a role of parental tolerance. *Proc. R. Soc. Lond. B Biol. Sci.* **269**, 1709–1713. (doi:10.1098/rspb.2002.2082)
- Bonte D, de la Peña E. 2009 Evolution of body condition-dependent dispersal in metapopulations. *J. Evol. Biol.* **22**, 1242–1251. (doi:10.1111/j.1420-9101.2009.01737.x)
- Gyllenberg M, Kisdi E, Utz M. 2011 Body condition dependent dispersal in a heterogeneous environment. *Theor. Popul. Biol.* **79**, 139–154. (doi:10.1016/j.tpb.2011.02.004)
- Li XY, Kokko H. 2018 Sex-biased dispersal: a review of the theory. *Biol. Rev.* **94**, 721–736.
- Dobson FS. 1982 Competition for mates and predominant juvenile male dispersal in mammals.

- Anim. Behav.* **30**, 1183–1192. (doi:10.1016/S0003-3472(82)80209-1)
15. Pusey AE. 1987 Sex-biased dispersal and inbreeding avoidance in birds and mammals. *Trends Ecol. Evol.* **2**, 295–299. (doi:10.1016/0169-5347(87)90081-4)
  16. Lawson-Handley L, Perrin N. 2007 Advances in our understanding of mammalian sex-biased dispersal. *Mol. Ecol.* **16**, 1559–1578. (doi:10.1111/j.1365-294X.2006.03152.x)
  17. Clarke AL, Sæther B-E, Røskoft E. 1997 Sex biases in avian dispersal: a reappraisal. *Oikos* **79**, 429–438. (doi:10.2307/3546885)
  18. Végvari Z, Katona G, Vagi B, Freckleton RP, Gaillard JM, Szekely L, Liker A. 2018 Sex-biased breeding dispersal is predicted by social environment in birds. *Ecol. Evol.* **8**, 6483–6491. (doi:10.1002/ece3.4095)
  19. Greenwood PJ. 1980 Mating systems, philopatry and dispersal in birds and mammals. *Anim. Behav.* **28**, 1140–1162. (doi:10.1016/S0003-3472(80)80103-5)
  20. Clutton-Brock TH (ed) 1988 *Reproductive success*. Chicago, IL: The University of Chicago Press.
  21. Fretwell SD, Lucas HJ. 1970 On territorial behavior and other factors influencing habitat distributions in birds. *Acta Biotheor.* **19**, 16–36. (doi:10.1007/BF01601953)
  22. Lidicker Jr WZ. 1975 The role of dispersal in the demography of small mammals. In *Small mammals: their production and population dynamics* (eds FB Golley, K Petruszewicz, L Ryszkowski), pp. 103–128. London, UK: Cambridge University Press.
  23. Fretwell SD. 1972 *Populations in a seasonal environment*. Princeton, NJ: Princeton University Press.
  24. Le Galliard J-F, Clobert J. 2003 Mother–offspring interactions affect natal dispersal in a lizard. *Proc. R. Soc. Lond. B* **270**, 1163–1169. (doi:10.1098/rspb.2003.2360)
  25. Martinig AR, McAdam AG, Dantzer B, Lane JE, Coltman DW, Boutin S. 2020 The new kid on the block: immigrant males win big whereas females pay fitness cost after dispersal. *Ecol. Lett.* **23**, 430–438. (doi:10.1111/ele.13436)
  26. Bonte D *et al.* 2012 Costs of dispersal. *Biol. Rev.* **87**, 290–312.
  27. Maag N, Cozzi G, Bateman A, Heistermann M, Ganswindt A, Manser M, Clutton-Brock T, Ozgul A. 2019 Cost of dispersal in a social mammal: body mass loss and increased stress. *Proc. R. Soc. BBiol. Sci.* **286**, 20190033. (doi:10.1098/rspb.2019.0033)
  28. Pettifor RA, Perrins CM, McCleery RH. 1988 Individual optimization of clutch size in great tits. *Nature* **336**, 160–162. (doi:10.1038/336160a0)
  29. Waser PM, Jones WT. 1983 Natal philopatry among solitary mammals. *Q. Rev. Biol.* **58**, 355–390. (doi:10.1086/413385)
  30. Edelman AJ. 2011 Sex-specific effects of size and condition on timing of natal dispersal in kangaroo rats. *Behav. Ecol.* **22**, 776–783. (doi:10.1093/beheco/arr050)
  31. Behr DM, McNutt JW, Ozgul A, Cozzi G. 2020 When to stay and when to leave? Proximate causes of dispersal in an endangered social carnivore. *J. Anim. Ecol.* **89**, 2356–2366. (doi:10.1111/1365-2656.13300)
  32. Andersen R, Duncan P, Linnell JDC. 1998 *The European roe deer: the biology of success*. Oslo, Norway: Scandinavian University Press.
  33. Strandgaard H. 1972 The roe deer (*Capreolus capreolus*) population at Kalø and the factors regulating its size. *Danish Rev. Game Biol.* **7**, 1–205.
  34. Wahlström LK. 1994 The significance of male–male aggression for yearling dispersal in roe reer (*Capreolus capreolus*). *Behav. Ecol. Sociobiol.* **35**, 409–412. (doi:10.1007/BF00165843)
  35. Coulon A, Cosson JF, Morellet N, Angibault JM, Cargnelutti B, Galan M, Aulagnier S, Hewison AJM. 2006 Dispersal is not female biased in a resource-defence mating ungulate, the European roe deer. *Proc. R. Soc. B* **273**, 341–348. (doi:10.1098/rspb.2005.3329)
  36. Gaillard JM *et al.* 2008 Population density and sex do not influence fine-scale natal dispersal in roe deer. *Proc. R. Soc. B Biol. Sci.* **275**, 2025–2030.
  37. Debeffe L, Morellet N, Cargnelutti B, Lourtet B, Bon R, Gaillard J-M, Hewison AJM. 2012 Condition-dependent natal dispersal in a large herbivore: heavier animals show a greater propensity to disperse and travel further. *J. Anim. Ecol.* **81**, 1327–1337. (doi:10.1111/j.1365-2656.2012.02014.x)
  38. Debeffe L, Morellet N, Verheyden-Tixier H, Hoste H, Gaillard JM, Cargnelutti B, Picot D, Sevila J, Hewison AJM. 2014a Parasite abundance contributes to condition-dependent dispersal in a wild population of large herbivore. *Oikos* **123**, 1121–1125. (doi:10.1111/oik.01396)
  39. Vanpé C *et al.* 2007 Antler size provides a honest signal of male phenotypic quality in roe deer. *Am. Nat.* **169**, 481–493. (doi:10.1086/512046)
  40. Wahlström LK, Kjellander F. 1995 Ideal free distribution and natal dispersal in female roe deer. *Oecologia* **103**, 302–308. (doi:10.1007/BF00328618)
  41. Pettorelli N, Gaillard JM, Duncan P, Maillard D, Van Laere G, Delorme D. 2003 Age and density modify the effects of habitat quality on survival and movements of roe deer. *Ecology* **84**, 3307–3316. (doi:10.1890/02-0602)
  42. Swenson JE, Sandegren F, SO-Derberg A. 1998 Geographic expansion of an increasing brown bear population: evidence for presaturation dispersal. *J. Anim. Ecol.* **67**, 819–826. (doi:10.1046/j.1365-2656.1998.00248.x)
  43. Gaillard JM, Boutin JM, Delorme D, Van Laere G, Duncan P, Lebreton JD. 1997 Early survival in roe deer: causes and consequences of cohort variation in two contrasted populations. *Oecologia* **112**, 502–513. (doi:10.1007/s004420050338)
  44. Kjellander P, Gaillard JM, Hewison AJM. 2006 Density-dependent responses of fawn cohort body mass in two contrasting roe deer populations. *Oecologia* **146**, 521–530. (doi:10.1007/s00442-005-0188-z)
  45. Baines CB, Travis MJM, McCauley SJ, Bocedi G. 2020 Negative density-dependent dispersal emerges from the joint evolution of density- and body-condition dependent dispersal strategies. *Evolution* **74**, 2238–2249. (doi:10.1111/evo.14085)
  46. Hewison AJM, Gaillard JM, Delorme D, Van Laere G, Amblard T, Klein F. 2011 Reproductive constraints, not environmental conditions, shape the ontogeny of sex-specific mass-size allometry in roe deer. *Oikos* **120**, 1217–1226. (doi:10.1111/j.1600-0706.2011.19316.x)
  47. Rousset F, Gandon S. 2002 Evolution of the distribution of dispersal distance under distance-dependent cost of dispersal. *J. Evol. Biol.* **15**, 515–523. (doi:10.1046/j.1420-9101.2002.00430.x)
  48. Toigo C, Gaillard JM, Van Laere G, Hewison M, Morellet N. 2006 How does environmental variation influence body mass, body size, and body condition? Roe deer as a case study. *Ecography* **29**, 301–308. (doi:10.1111/j.2006.0906-7590.04394.x)
  49. Hewison AJM, Vincent JP, Angibault JM, Delorme D, Van Laere G, Gaillard JM. 1999 Tests of age estimation from tooth wear on roe deer of known age: variation within and between populations. *Can. J. Zool.* **77**, 58–67. (doi:10.1139/z98-183)
  50. Morellet N, Verheyden H, Angibault JM, Cargnelutti B, Lourtet B, Hewison AJM. 2009 The effect of capture on ranging behaviour and activity of the European roe deer *Capreolus capreolus*. *Wildl. Biol.* **15**, 278–287. (doi:10.2981/08-084)
  51. Ducros D *et al.* 2020 Beyond dispersal versus philopatry? Alternative behavioural tactics of juvenile roe deer in a heterogeneous landscape. *Oikos* **129**, 81–92. (doi:10.1111/oik.06793)
  52. Hewison AJM, Gaillard JM, Angibault JM, Van Laere G, Vincent JP. 2002 The influence of density on post-weaning growth in roe deer *Capreolus capreolus* fawns. *J. Zool.* **257**, 303–309. (doi:10.1017/S0952836902000900)
  53. Burnham KP, Anderson DR. 2002 *Model selection and multimodel inference — a practical information theoretic approach*, 2nd edn. New York, NY: Springer-Verlag.
  54. Pinheiro J, Bates D. 2000 *Mixed-effects models in S and S-PLUS*. New York, NY: Springer-Verlag.
  55. R Development Core Team. 2019 *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing <http://www.R-project.org/>.
  56. Pinheiro J, Bates D, DebRoy S, Sarkar D, R-core. 2016 nlme: Linear and nonlinear mixed effects models. R package version 3.1. <https://CRAN.R-project.org/package=nlme>.
  57. Bartoň K. 2016 MuMIn: Multi-Model Inference. R-package version 1.15.6.
  58. Perrin N, Mazalov V. 2000 Local competition, inbreeding, and the evolution of sex-biased dispersal. *Am. Nat.* **155**, 116–127. (doi:10.1086/303296)
  59. Matthysen E. 2005 Density-dependent dispersal in birds and mammals. *Ecography* **28**, 403–416. (doi:10.1111/j.0906-7590.2005.04073.x)
  60. Maag N, Cozzi G, Clutton-Brock T, Ozgul A. 2018 Density-dependent dispersal strategies in a cooperative breeder. *Ecology* **99**, 1932–1941. (doi:10.1002/ecy.2433)



61. Garel M, Gaillard J-M, Jullien J-M, Dubray D, Maillard D, Loison A. 2011 Population abundance and early spring conditions determine variation in body mass of juvenile chamois. *J. Mammal.* **92**, 1112–1117. (doi:10.1644/10-MAMM-A-056.1)
62. Hewison AJM *et al.* 2009 Landscape fragmentation influences winter body mass of roe deer. *Ecography* **32**, 062–1070.
63. Matthysen E. 2012 Multicausality of dispersal: a review. In *Dispersal ecology and evolution* (eds J Clobert, M Baguette, TG Benton, JM Bullock), pp. 3–18. Oxford, UK: Oxford University Press.
64. Davis JM, Stamps JA. 2004 The effect of natal experience on habitat preferences. *Trends Ecol. Evol.* **19**, 411–416. (doi:10.1016/j.tree.2004.04.006)
65. Le Galliard J-F, Ferrière R, Clobert J. 2005 Effect of patch occupancy on immigration in the common lizard. *J. Anim. Ecol.* **74**, 241–249. (doi:10.1111/j.1365-2656.2005.00912.x)
66. Garant D, Kruuk LE, Wilkin TA, McCleery RH, Sheldon BC. 2005 Evolution driven by differential dispersal within a wild bird population. *Nature* **433**, 60–65. (doi:10.1038/nature03051)
67. Vanpé C, Morellet N, Kjellander P, Goulard M, Liberg O, Hewison AJM. 2009 Access to mates in a territorial ungulate is determined by the size of a male's territory, but not by its habitat quality. *J. Anim. Ecol.* **78**, 42–51. (doi:10.1111/j.1365-2656.2008.01467.x)
68. Perrin N, Goudet J. 2001 Inbreeding, kinship, and the evolution of natal dispersal. In *Dispersal* (eds J Clobert, E Danchin, AA Dhondt, J Nichols), pp. 123–142. New York, NY: Oxford university press.
69. Debeffe L *et al.* 2014 A one night stand? Reproductive excursions of female roe deer as a breeding dispersal tactic. *Oecologia* **176**, 431–443. (doi:10.1007/s00442-014-3021-8)
70. Gyllenberg M, Kisdi E, Utz M. 2008 Evolution of condition-dependent dispersal under kin competition. *J. Math. Biol.* **57**, 285–307. (doi:10.1007/s00285-008-0158-2)
71. Wahlström K, Liberg O. 1995 Contrasting dispersal patterns in two Scandinavian roe deer *Capreolus capreolus* populations. *Wildl. Biol.* **1**, 159–164. (doi:10.2981/wlb.1995.020)
72. Loe LE, Mysterud A, Veiberg V, Langvatn R. 2009 Negative density-dependent emigration of males in an increasing red deer population. *Proc. R. Soc. B* **276**, 2581–2587. (doi:10.1098/rspb.2009.0224)
73. Loe LE, Mysterud A, Veiberg V, Langvatn R. 2010 No evidence of juvenile body mass affecting dispersal in male red deer. *J. Zool.* **280**, 84–91. (doi:10.1111/j.1469-7998.2009.00647.x)
74. Lambin X, Aars J, Piertney SB. 2001 Dispersal, intraspecific competition, kin competition and kin facilitation: a review of empirical evidence. In *Dispersal* (eds J Clobert, E Danchin, AA Dhondt, J Nichols), pp. 110–122. New York, NY: Oxford university press.
75. Benoit L, Hewison AJM, Coulon A, Debeffe L, Gremillet D, Ducros D, Cargnelutti B, Chaval Y, Morellet N. 2020 Accelerating across the landscape: the energetic costs of natal dispersal in a large herbivore. *J. Anim. Ecol.* **89**, 173–185. (doi:10.1111/1365-2656.13098)
76. Barbraud C, Delor K. 2020 Selection against immigrants in wild seabird populations. *Ecol. Lett.* **24**, 84–93. (doi:10.1111/ele.13624)
77. Johnson CA, Fryxell JM, Thompson ID, Baker JA. 2009 Mortality risk increases with natal dispersal distance in American martens. *Proc. R. Soc. B* **276**, 3361–3367. (doi:10.1098/rspb.2008.1958)
78. Stamps JA, Krishnan VV, Reid ML. 2005 Search costs and habitat selection by dispersers. *Ecology* **86**, 510–518. (doi:10.1890/04-0516)
79. Delgado MD, Penteriani V, Revilla E, Nams VO. 2010 The effect of phenotypic traits and external cues on natal dispersal movements. *J. Anim. Ecol.* **79**, 620–632. (doi:10.1111/j.1365-2656.2009.01655.x)
80. Forrester TD, Casady DS, Wittmer HU. 2015 Home sweet home: fitness consequences of site familiarity in female black-tailed deer. *Behav. Ecol. Sociobiol.* **69**, 603–612. (doi:10.1007/s00265-014-1871-z)
81. McNamara JM, Houston AI. 1996 State-dependent life histories. *Nature* **380**, 215–221.
82. Gaillard JM, Liberg O, Andersen R, Hewison AJM. 1998 Population dynamics of roe deer. In *The European roe deer: the biology of success* (eds R Andersen, P Duncan, JDC Linnell), pp. 309–335. Oslo, Norway: Scandinavian University Press.
83. Hewison AJM. 2021 Data from: Dispersal propensity and distance in relation to sex and body mass of roe deer. Dryad Digital Repository (<https://doi.org/10.5061/dryad.nvx0k6drh>)