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Does your article include research that required ethical approval or permits?:
Yes

Statement (if applicable):
The protocol for animal capture and handling was established in accordance with local and European animal welfare laws (prefectural order from the Toulouse Administrative Authority to capture and monitor wild roe deer and agreement no. A31113001 approved by the Departmental Authority of Population Protection).

Data

It is a condition of publication that data, code and materials supporting your paper are made publicly available. Does your paper present new data?:
Yes

Statement (if applicable):
All raw data are stored in the EURODEER spatial data base 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 (doi: 10.5061/dryad.nvx0k6drh).

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I/We declare we have no competing interests

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AJMH, SF, JMG, LD and PK conceived the project, with the participation of BG, MK and MH. BC, AJMH, NM, LD, and AC collected the data. SF and NM collated and analysed the data. AJMH wrote the manuscript with input from all authors who also gave final approval for publication.

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

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Abstract

Evolution should favour plasticity in dispersal decisions in response to spatial heterogeneity in social and environmental contexts. Sex differences in individual optimisation 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 south-west 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. In 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 behaviour of males and females. We suggest that females disperse prior to habitat saturation being reached, likely in relation to the risk of inbreeding. In 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.

Key words: body mass; individual optimisation; philopatry; roe deer;

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 (Clobert et al. 2012, Ronce 2007). Furthermore, dispersal is a key component of a species' response to global change (Berg et al. 2010), facilitating shifts in geographic range in response to rapid and wide-scale modifications of suitable environmental conditions (Parmesan et al. 1999). Dispersal is driven by inbreeding avoidance, resource competition, particularly among kin, and habitat heterogeneity (Clobert et al. 2012, Bowler and Benton 2005). 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* Ims and Hjermann 2001). Condition dependence occurs when dispersal behaviour is influenced by any internal state variable (Dufty and Belthoff 2001, Massot et al. 2002), for example, an individual's sex (Trochet et al. 2016), age (Ekman and Griesser 2002) or body condition (Bonte and de la Peña 2009, Gyllenberg et al. 2011).

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 (Trochet et al. 2016, Li & Kokko 2018). For example, dispersal is male-biased in most mammals (Dobson 1982, Pusey 1987, Lawson-Handley and Perrin 2007), whereas it is generally female-biased in birds

(Clarke et al. 1997, Végvari et al. 2018). This difference is potentially linked to differences in mating tactic, social environment, sexual size dimorphism or asymmetry in parental care (Greenwood 1980, Lawson-Handley and Perrin 2007, Trochet et al. 2016). In polygynous species, females are generally limited by scramble competition for resources to offset the costs of reproduction (Clutton-Brock 1988). 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* Fretwell and Lucas 1970). 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 (Lidicker 1975). In contrast, because polygynous males are limited by breeding opportunities in terms of access to females through male-male contest competition (Clutton-Brock 1988), dispersal is expected to be enforced, resulting from competitive exclusion by dominant individuals (Fretwell 1972). This dichotomy in life history constraints between the sexes should drive the evolution of divergent sex-specific dispersal tactics (Le Galliard and Clobert 2003, Martinig et al. 2020).

Given that dispersal is costly (Bonte et al. 2012, for a case study see Maag et al. 2019), individuals are expected to optimize their dispersal tactics (individual optimization *sensu* Pettifor et al. 1988) 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 (Waser and Jones 1983), species where both sexes commonly disperse provide ideal model systems to identify sex-specific drivers governing condition-dependent dispersal decisions (e.g. Edelman 2011, Behr et al. 2020).

One such species is the roe deer, which is widely distributed across Europe and has been intensively studied over much of its range (Andersen et al. 1998), especially with regards to natal dispersal (e.g. Strandgaard 1972, Wahlström 1994). Recent studies have indicated that natal dispersal of roe deer is equally prevalent in both sexes (Coulon et al. 2006, Gaillard et al. 2008), does not fluctuate with population density (Gaillard et al. 2008), and increases with body condition (Debeffe et al. 2012, 2014a), 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 (Wahlström 1994). Resident territorial males direct most of their aggressive interactions towards the most sexually mature juveniles with larger than average antlers (Wahlström 1994), which are also heavier (Vanpé et al. 2007), presumably because these individuals pose the most threat in terms of territory loss. In contrast, female roe deer are not territorial and were initially reported to be distributed according to an ideal free distribution (Wahlström and Kjellander 1995), although subsequent investigations did not support this (Pettorelli et al. 2003). Gaillard et al. (2008) 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 (Swenson et al. 1998),dispersal in roe deer might peak during the pre-saturation phase, prior to the carrying capacity of the habitat being reached (sensu Lidicker 1975). 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 (Gaillard et al. 1997) that decreases with increasing density-dependent competition for resources (Kjellander et al. 2006). Following Wahlström (1994), 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 (Baines et al. 2020). As density increases so that average body condition decreases, *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 (Debeffe et al. 2012). Finally, sexual size dimorphism of roe deer is rather weak (adult males weigh only 10% more than females, Hewison et al. 2011) so that dispersal is likely equally energetically costly for both sexes (Rousset and Gandon 2002). Because heavier animals are in better condition in an income breeder such as roe deer (Toïgo et al. 2006), 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 (Bonte et al. 2012). Hence, we expected dispersal distance to increase with body mass and in a similar manner for both sexes.

Materials and methods

Study system

We quantified natal dispersal of 146 GPS monitored juvenile roe deer (68 males, 78 females) in an intensively monitored population in Vallons et Coteaux de Gascogne (Zone Atelier PyGar), south-west 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 8 individuals / 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% (c. 130 individuals) of the population is removed by hunting each year (unpublished data from the Hunting Regional Agency).

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, Hewison et al. 1999), 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 hour intervals year-round, before being released on site. We removed all GPS fixes taken during the first eight days after capture because of the potential disruption of normal spatial behaviour due to capture (Morellet et al. 2009), and GPS fixes for which the location was obviously erroneous (0.0003% of the location data set) 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 n° A31113001).

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 (Strandgaard 1972, Debeffe et al. 2012). Because roe deer juveniles remain strongly associated with their mothers during their first year of life, and because adult females are highly sedentary (Andersen et al. 1998), 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 (Ducros et al. 2020): 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 Ducros et al. 2020 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) vs. 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.

Standardising body mass to 1st February

The body mass of juvenile roe deer may fluctuate over their first winter in relation to the onset and duration of winter (Hewison et al. 2002). 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 (24th November JD = 0; 5th March JD = 101). Because, on average, males weigh slightly more than females (Hewison et al. 2011), we included sex as an additive effect in this model. We then used the regression coefficient of the common slope to standardise individual body mass by date for both sexes (i.e. conserving sexual size dimorphism), expressed as the predicted body mass on 1st February (JD = 32, approx. median date of capture).

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 1st 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 1st February and sex in the most complex model. We then performed model selection using AICc to identify the model that best fit the data (Burnham and Anderson 2002). 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.

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 (Pinheiro and Bates 2000) to model dispersal distance as a function of individual body mass on 1st 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, Pinheiro and Bates 2000). 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 (R Development Core Team. 2019). All generalized least squares models were fitted using the “gls” function in the “nlme” library (Pinheiro et al. 2016). We used the “dredge” function in the MuMIn library (Bartoń 2016) to generate the set of candidate models that we defined a priori based on our biological hypotheses (see above).

Results

Dispersal propensity

The model containing the main effect of sex only was not competitive compared to the null model (ΔAICc = 1.79, 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 1st February and, based on AICc weights, was about three times as likely to adequately describe the data as the second best model (ΔAICc = 2.36), which included the simple effect of body mass only (Table S1). In males, dispersal propensity increased markedly with increasing body mass so that dispersal propensity increased more than 8-fold (from less than 10% to around 80%) over the recorded range of body mass (Fig. 1, see Table 1 for parameter estimates). A threshold model of this relationship indicated some support for a break point 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. In contrast, dispersal propensity in females was approximately constant irrespective of body mass (Fig. 1) such that heavy females dispersed with approximately the same probability as lighter females. This was the case irrespectively of whether body mass was included as, alternatively, either a linear, a quadratic or a threshold function (ΔAICc with the null model > 2).

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 (Fig. 2). The best model explaining observed variation in dispersal distance included an effect of body mass on 1st February only, and was about three times as likely to adequately describe the data as the second best model (ΔAICc = 2.12), which included the additive effects of body mass and sex (Table S2). Dispersal distance increased with body mass in both sexes (Fig. 3, see Table 1), and this increase was of a similar magnitude in males and females (estimated difference in slope of 0.66 ± sd 1.60 km/kg, P = 0.68). Heavy (>16 kg, males and females combined) dispersers travelled around twice as far as light (<16 kg) dispersers (mean ± sd: light = 5.3 ± 9.5 km, range: 0.4 – 43.1 km; heavy = 11.3 ± 13.8 km, range: 0.3 – 56.4 km), irrespective of their sex.

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 sex-specific (Perrin and Mazalov 2000). Species of mammals in which natal dispersal is equally prevalent in both sexes are rare (Waser and Jones 1983), 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. In contrast, females emigrated from their natal range irrespective of their body mass, but among those that did disperse, heavier individuals travelled farther. We suggest that this sex-specific pattern is due to different selection pressures acting on dispersal behaviour of males and females (Perrin and Mazalov 2000, Martinig et al. 2020). 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.

Dispersal and local resource competition in females

Emigration has been frequently observed to increase with resource competition (Bowler & Benton 2005, Matthysen 2005, Maag et al. 2018). Body mass of juveniles during their first winter is a highly informative metric of resource limitation in large herbivores in general (Garel et al. 2011) and in roe deer in particular (Toïgo et al. 2006). 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 (Gaillard et al. 1997). 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 Baines et al. 2020), 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 (Fig. 1). We suggest that female roe deer disperse independently of habitat saturation and, as a result, irrespectively of population density (Gaillard et al. 2008). Instead, 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 pattern similar to that previously reported for brown bears (Swenson et al. 1998). 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 (Hewison et al. 2009).

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* (Fig. 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 ± 2.2 km for a female juvenile that was 2 kg heavier than average, compared to 7.0 ± 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 (Matthysen 2012), potentially using similarity with the natal range as a cue for identifying a suitable habitat patch (Natal Habitat Preference Induction, *sensu* Davis & Stamps 2004). Successful settlement has been shown to depend on body condition, with larger or heavier individuals successfully accessing already populated habitat in lizards (Le Galliard et al. 2005) or habitat patches of higher quality in great tits (Garant et al. 2005).

While we hypothesise 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 (Vanpé et al. 2009). 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 (Perrin and Goudet 2001). 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 (Debeffe et al. 2014b). Indeed, by coupling kin recognition with mate choice, females can avoid inbreeding without incurring some of the costs linked to true dispersal (see Behr et al. 2020 for a similar argument in male African wild dog).

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 local competition is strong (Gyllenberg et al. 2008, Bonte and de la Peña 2009). Wahlström (1994) 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 (Wahlström & Liberg 1995) as *dispersal propensity* consistently increased with body mass in male juveniles. In contrast, Loe et al. (2009, 2010) 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. (2008) demonstrated that dispersal of competitively strong individuals may be a common outcome under kin competition (e.g. Edelman 2011 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. Lambin et al. 2001). Roe deer males are strongly territorial from March to September, defending a mating territory concomitantly with the entire period when juveniles disperse and settle (Vanpé et al. 2009). 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 (Fretwell 1972), with males dispersing until they locate the nearest vacant territory that will provide access to reproductive females (Vanpé et al. 2009).

Individual quality and the cost of dispersal

Individuals should optimise dispersal decisions in relation to both condition-dependent competitive ability and costs (Gyllenberg et al. 2008). 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 15km). 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 (Benoit et al. 2020). During both transience and settlement, dispersers are also likely to suffer missed feeding opportunities (Benoit et al. 2020) and greater stress (Maag et al. 2019), likely generating substantial life history costs (e.g. Barbraud and Delord 2020). In agreement, Johnson et al. (2009) 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 (Stamps et al. 2005). 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 (Delgado et al. 2010). Opportunity costs (*sensu* Bonte et al. 2012) for dispersers due to loss of familiarity with the environment may, indeed, be substantial (Forrester et al. 2015).

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 optimisation 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 McNamara and Houston 1996) whereby an individual makes decisions with adaptive consequences based on its condition. Body mass attained prior to dispersal predicts survival and adult mass (Gaillard et al. 1998) 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 Benoit et al. 2020), irrespective of their sex. In 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 data base 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 (doi: 10.5061/dryad.nvx0k6drh).

Authors' contributions

AJMH, SF, JMG, LD and PK conceived the project, with the participation of BG, MK and MH. BC, AJMH, NM, LD, and AC collected the data. SF and NM collated and analysed the data. AJMH wrote the manuscript with input from all authors who also gave final approval for publication.

Competing interests

We declare that we have no competing interests.

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Footnotes

Electronic supplementary material is available online at (doi: xxxx.xxxx).

References

Andersen, R., P. Duncan, and J. D. C. Linnell. 1998. The European roe deer: the biology of success. Scandinavian University Press, Oslo.

Baines, C.B., J.M.J. Travis, S.J. McCauley, and G. Bocedi. 2020. Negative density-dependent dispersal emerges from the joint evolution of density- and body-condition dependent dispersal strategies. Evolution 74:2238-2249.

Barbraud, C., and K. Delord. 2020. Selection against immigrants in wild seabird populations. Ecology Letters doi: 10.1111/ele.13624.

Bartoń, K. 2016. MuMIn: Multi-Model Inference. R-package version 1.15.6.

Behr, D.M., J.W. McNutt, A. Ozgul, and G. Cozzi. 2020. When to stay and when to leave? Proximate causes of dispersal in an endangered social carnivore. Journal of Animal Ecology 89:2356-2366.

Benoit, L., A.J.M. Hewison, A. Coulon, L. Debeffe, D. Gremillet, D. Ducros, B. Cargnelutti, Y. Chaval, and N. Morellet, 2020. Accelerating across the landscape: the energetic costs of natal dispersal in a large herbivore. Journal of Animal Ecology 89:173-185.

Berg, M. P., E. Kiers, G. Driessen, M. Van Der Heijden, B. W. Kooi, F. Kuenen, M. Liefting, H. A. Verhoef, and J. Ellers. 2010. Adapt or disperse: understanding species persistence in a changing world. Global Change Biology 16:587–598.

Bonte, D., and E. de la Peña. 2009. Evolution of body condition-dependent dispersal in metapopulations. Journal of Evolutionary Biology 22:1242–1251.

Bonte, D., H. Van Dyck, J. M. Bullock, A. Coulon, M. Delgado, M. Gibbs, V. Lehouck, E. Matthysen, K. Mustin, M. Saastamoinen, N. Schtickzelle, V. M. Stevens, S. Vandewoestijne, M. Baguette, K. Barton, T. G. Benton, A. Chaput-Bardy, J. Clobert, C.

Dytham, T. Hovestadt, C. M. Meier, S. C. F. Palmer, C. Turlure, and J. M. J. Travis. 2012. Costs of dispersal. Biological Reviews 87:290–312.

Bowler, D. E., and T. G. Benton. 2005. Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. Biological Reviews 80:205–225.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference - A practical information theoretic approach. 2d edition. Springer-Verlag, New York.

Clarke, A. L., B.-E. Sæther, and E. Røskaft. 1997. Sex biases in avian dispersal: a reappraisal. Oikos:429–438.

Clobert, J., M. Baguette, T. G. Benton, and J. M. Bullock. 2012. Dispersal Ecology and Evolution. Oxford University Press, Oxford, New York.

Clutton-Brock, T. H., editor. 1988. Reproductive success. The University of Chicago Press, Chicago, IL, USA.

Coulon, A., J. F. Cosson, N. Morellet, J. M. Angibault, B. Cargnelutti, M. Galan, S. Aulagnier, and A. J. M. Hewison. 2006. Dispersal is not female biased in a resource-defence mating ungulate, the European roe deer. Proceedings of the Royal Society B-Biological Sciences 273:341–348.

Davis, J.M. and J.A. Stamps. 2004. The effect of natal experience on habitat preferences. Trends in Ecology and Evolution 19:411-416.

Debeffe, L., N. Morellet, B. Cargnelutti, B. Lourtet, R. Bon, J.-M. Gaillard, and A. J. M. Hewison. 2012. Condition-dependent natal dispersal in a large herbivore: heavier animals show a greater propensity to disperse and travel further. Journal of Animal Ecology 81:1327–1337.

Debeffe, L., N. Morellet, H. Verheyden-Tixier, H. Hoste, J. M. Gaillard, B. Cargnelutti, D. Picot, J. Sevila, and A. J. M. Hewison. 2014a. Parasite abundance contributes to condition-dependent dispersal in a wild population of large herbivore. Oikos 123:1121–1125.

Debeffe, L., S. Focardi, C. Bonenfant, N. Morellet, A. J. M. Hewison, J. D. . Linnell, M. Heurich, P. Sustr, P. Kjellander, A. Mysterud, F. Urbano, M. Pellerin, C. Vanpé, and F. Cagnacci. 2014b. A one night stand? Reproductive excursions of female roe deer as a breeding dispersal tactic. Oecologia 176:431–443.

Delgado, M. D., V. Penteriani, E. Revilla, and V. O. Nams. 2010. The effect of phenotypic traits and external cues on natal dispersal movements. Journal of Animal Ecology 79:620–632.

Dobson, F. S. 1982. Competition for mates and predominant juvenile male dispersal in mammals. Animal behaviour 30:1183–1192.

Ducros, D., N. Morellet, R. Patin, K. Atmeh, L. Debeffe, B. Cargnelutti, Y. Chaval, B. Lourtet, A. Coulon and A.J.M. Hewison. 2020. Beyond dispersal versus philopatry? Alternative behavioural tactics of juvenile roe deer in a heterogeneous landscape. Oikos 129:81-92.

Dufty, A. M., and J. R. Belthoff. 2001. Proximate mechanisms of natal dispersal: the role of body condition and hormones. Pages 217–229*in* J. Clobert, E. Danchin, A. A. Dhondt, and J. D. Nichos, editors.Dispersal. Oxford university press, New York.

Edelman, A. J. 2011. Sex-specific effects of size and condition on timing of natal dispersal in kangaroo rats. Behavioral Ecology 22:776–783.

Ekman, J., and M. Griesser. 2002. Why offspring delay dispersal: experimental evidence for a role of parental tolerance. Proceedings of the Royal Society of London B: Biological Sciences 269:1709–1713.

Forrester, T.D., D.S. Casady and H.U. Wittmer. 2015. Home sweet home: fitness consequences of site familiarity in female black-tailed deer. Behavioural Ecology and Sociobiology 69:603-612.

Fretwell, S. D. 1972. Populations in a seasonal environment. Princeton University Press.

Fretwell, S. D., and H. J. Lucas. 1970. On territorial behavior and other factors influencing habitat distributions in birds. Acta Biotheoretica 19:16–36.

Gaillard, J.M., J.M. Boutin, D. Delorme, G. Van Laere, P. Duncan, and J.D. Lebreton. 1997. Early survival in roe deer : causes and consequences of cohort variation in two contrasted populations. Oecologia 112:502-513.

Gaillard, J. M., A. J. M. Hewison, P. Kjellander, N. Pettorelli, C. Bonenfant, B. Van Moorter, O. Liberg, H. Andren, G. Van Laere, F. Klein, J. M. Angibault, A. Coulon, and C. Vanpe. 2008. Population density and sex do not influence fine-scale natal dispersal in roe deer. Proceedings of the Royal Society B-Biological Sciences 275:2025–2030.

Garant, D., L. E. Kruuk, T. A. Wilkin, R. H. McCleery, and B. C. Sheldon. 2005. Evolution driven by differential dispersal within a wild bird population. Nature 433:60–65.

Garel, M., J.-M. Gaillard, J.-M. Jullien, D. Dubray, D. Maillard, and A. Loison. 2011. Population abundance and early spring conditions determine variation in body mass of juvenile chamois. Journal of Mammalogy 92:1112–1117.

Greenwood, P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. Animal Behaviour 28:1140–1162.

Gyllenberg, M., E. Kisdi, and M. Utz. 2008. Evolution of condition-dependent dispersal under kin competition. Journal of Mathematical Biology 57:285–307.

Gyllenberg, M., E. Kisdi, and M. Utz. 2011. Body condition dependent dispersal in a heterogeneous environment. Theoretical Population Biology 79:139–154.

Hewison, A. J. M., J. M. Gaillard, J. M. Angibault, G. Van Laere, and J. P. Vincent. 2002. The influence of density on post-weaning growth in roe deer *Capreolus capreolus* fawns. Journal of Zoology 257:303–309.

Hewison, A.J.M., J.P. Vincent, J.M. Angibault, D. Delorme, G. Van Laere and J.M. Gaillard. 1999. Tests of age estimation from tooth wear on roe deer of known age: variation within and between populations. Canadian Journal of Zoology 77:58–67.

Hewison, A.J.M., N. Morellet, H. Verheyden, T. Daufresne, J.M. Angibault, B. Cargnelutti, J. Merlet, D. Picot, J.L. Rames, J. Joachim, B. Lourtet, E. Serrano, E. Bideau and N. Cebe. 2009. Landscape fragmentation influences winter body mass of roe deer. Ecography 32: 062-1070.

Hewison, A.J.M., J.M. Gaillard, D. Delorme, G. Van Laere, T. Amblard and F. Klein. 2011. Reproductive constraints, not environmental conditions, shape the ontogeny of sex-specific mass-size allometry in roe deer. Oikos 120:1217-1226.

Hewison, A.J.M., N. Morellet, L. Debeffe, B. Cargnelutti and A.Coulon. 2021. Data from: Sex differences in condition-dependence of natal dispersal in a large herbivore: dispersal propensity and distance are decoupled. Dryad Digital Repository. (doi: 10.5061/dryad.nvx0k6drh)

Ims, R. A., and D. O. Hjermann. 2001. Condition-dependent dispersal. Pages 203–216*in* J. Clobert, E. Danchin, A. A. Dhondt, and J. D. Nichos, editors.Dispersal. Oxford university press, New York.

Johnson, C.A., J.M. Fryxell, I.D. Thompson, and J.A. Baker. 2009.Mortality risk increases with natal dispersal distance in American martens. Proceedings of the Royal Society B-Biological Sciences 276: 3361-3367.

Kjellander, P., J.M. Gaillard & A.J.M. Hewison. 2006. Density-dependent responses of fawn cohort body mass in two contrasting roe deer populations. Oecologia 146:521-530.

Lambin, X., J. Aars, and S. B. Piertney. 2001. Dispersal, intraspecific competition, kin competition and kin facilitation: a review of empirical evidence. Pages 110–122*in* J. Clobert, E. Danchin, A. A. Dhondt, and J. Nichols, editors.Dispersal. Oxford university press, New York.

Lawson-Handley, L., and N. Perrin. 2007. Advances in our understanding of mammalian sex-biased dispersal. Molecular Ecology 16:1559–1578.

Le Galliard, J.-F., and J. Clobert. 2003. Mother–offspring interactions affect natal dispersal in a lizard. Proceedings of the Royal Society of London B: Biological Sciences 270:1163–1169.

Le Galliard, J.-F., R. Ferrière, and J. Clobert. 2005. Effect of patch occupancy on immigration in the common lizard. Journal of Animal Ecology 74:241–249.

Li, X.Y. and H. Kokko. 2018. Sex-biased dispersal: a review of the theory. Biological Reviews 94:721-736.

Lidicker W. Z. Jr 1975. The role of dispersal in the demography of small mammals. In: Small mammals: their production and population dynamics. F. B. Golley, K. Petrusewicz and L. Ryszkowski, eds. Cambridge University Press, London: 103–128.

Loe, L. E., A. Mysterud, V. Veiberg, and R. Langvatn. 2010. No evidence of juvenile body mass affecting dispersal in male red deer. Journal of Zoology 280:84–91.

Loe, L. E., A. Mysterud, V. Veiberg, and R. Langvatn. 2009. Negative density-dependent emigration of males in an increasing red deer population. Proceedings of the Royal Society B-Biological Sciences 276:2581–2587.

Maag, N., G. Cozzi, T. Clutton-Brock, and A. Ozgul. 2018. Density-dependent dispersal strategies in a cooperative breeder. Ecology 99:1932-1941.

Maag, N., G. Cozzi, A. Bateman, M. Heistermann, A. Ganswindt, M. Manser, T. Clutton-Brock, and A. Ozgul. 2019. Cost of dispersal in a social mammal: body mass loss and increased stress. Proceedings of the Royal Society B-Biological Sciences 286: doi.org/10.1098/rspb.2019.0033.Massot, M., J. Clobert, P. Lorenzon, and J. M. Rossi. 2002. Condition-dependent dispersal and ontogeny of the dispersal behaviour: an experimental approach. Journal of Animal Ecology 71:253–261.

Martinig, A.R., A.G. McAdam, B. Dantzer, J.E. Lane, D.W. Coltman, and S. Boutin. 2020. The new kid on the block: immigrant males win big whereas females pay fitness cost after dispersal. Ecology Letters 23:430-438.

Matthysen, E. 2005. Density-dependent dispersal in birds and mammals. Ecography 28:403–416.

Matthysen, E. 2012. Multicausality of dispersal: a review. Pages 3–18*in* J. Clobert, M. Baguette, T. G. Benton, and J. M. Bullock, editors. Dispersal Ecology and Evolution. Oxford University Press, Oxford, United Kingdom.

Morellet, N., H. Verheyden, J. M. Angibault, B. Cargnelutti, B. Lourtet, and A. J. M. Hewison. 2009. The effect of capture on ranging behaviour and activity of the European roe deer Capreolus capreolus. Wildlife Biology 15:278–287.

Parmesan, C., N. Ryrholm, C. Stefanescu, J. K. Hill, C. D. Thomas, H. Descimon, B. Huntley, L. Kaila, J. Kullberg, and T. Tammaru. 1999. Poleward shifts in geographical ranges of butterfly species associated with regional warming. Nature 399:579–583.

Perrin, N., and J. Goudet. 2001. Inbreeding, kinship, and the evolution of natal dispersal. Pages 123–142*in* J. Clobert, E. Danchin, A. A. Dhondt, and J. Nichols, editors.Dispersal. Oxford university press, New York.

Perrin, N., and V. Mazalov. 2000. Local competition, inbreeding, and the evolution of sex-biased dispersal. The American Naturalist 155:116–127.

Pettifor, R.A., C.M. Perrins, and R.H. McCleery. 1988. Individual optimization of clutch size in great tits. Nature 336:160-162.

Pettorelli N., J.M. Gaillard, P. Duncan, D. Maillard, G. Van Laere, and D. Delorme 2003. Age and density modify the effects of habitat quality on survival and movements of roe deer. Ecology 84:3307-3316.

Pinheiro, J., and D. Bates. 2000. Mixed-effects models in S and S-PLUS. Springer Science and Business Media.

Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar, and R-core. 2016. nlme: Linear and nonlinear mixed effects models. R package version 3.1. URL https://CRAN.R-project.org/package=nlme

Pusey, A.E. 1987. Sex-biased dispersal and inbreeding avoidance in birds and mammals. Trends in Ecology and Evolution 2:295-299.

R Development Core Team. 2019. R: a language and environment for statistical computing. R Foundation for Statistical Computing,Vienna, Austria. URL http://www.R-project.org/.

Ronce, O. 2007. How does it feel to be like a rolling stone? Ten questions about dispersal evolution. Annual Review of Ecology Evolution and Systematics 38:231–253.

Rousset, F., and S. Gandon. 2002. Evolution of the distribution of dispersal distance under distance-dependent cost of dispersal. Journal of Evolutionary Biology 15:515–523.

Stamps, J. A., V. V. Krishnan, and M. L. Reid. 2005. Search costs and habitat selection by dispersers. Ecology 86:510–518.

Strandgaard, H. 1972 The roe deer (*Capreolus capreolus*) population at Kalø and the factors regulating its size. *Danish Review of Game Biology* 7:1-205

Swenson, J. E., F. Sandegren, and A. SO-Derberg, A. 1998. Geographic expansion of an increasing brown bear population: evidence for presaturation dispersal. Journal of Animal Ecology, 67:819-826.

Toïgo, C., J. M. Gaillard, G. Van Laere, M. Hewison, and N. Morellet. 2006. How does environmental variation influence body mass, body size, and body condition? Roe deer as a case study. Ecography 29:301–308.

Trochet, A., E. A. Courtois, V. M. Stevens, M. Baguette, A. Chaine, D. S. Schmeller, J. Clobert, and J. J. Wiens. 2016. Evolution of sex-biased dispersal. The Quarterly Review of Biology 91:297–320.

Vanpé, C., J-M.Gaillard, P. Kjellander, A. Mysterud, P. Magnien, D. Delorme, G. Van Laere, F. Klein, O. Liberg, and A.J.M. Hewison, 2007. Antler size provides a honest signal of male phenotypic quality in roe deer. American Naturalist 169:481-493.

Vanpé, C., N. Morellet, P. Kjellander, M. Goulard, O.Liberg, and A. J. M. Hewison. 2009. Access to mates in a territorial ungulate is determined by the size of a male's territory, but not by its habitat quality. Journal of Animal Ecology 78:42–51.

Végvari, Z., G. Katona, B. Vagi, R.P. Freckleton, J.M. Gaillard, *T.* Szekely and A. Liker. 2018. Sex-biased breeding dispersal is predicted by social environment in birds. Ecology and Evolution 8: 6483–6491.

Wahlström, K., and O. Liberg. 1995. Contrasting dispersal patterns in two Scandinavian roe deer Capreolus capreolus populations. Wildlife Biology 1:159–164.

Wahlström, L. K. 1994. The significance of male male-aggression for yearling dispersal in roe reer (*Capreolus-capreolus*). Behavioral Ecology and Sociobiology 35:409–412.

Wahlström, L. K., and F. Kjellander. 1995. Ideal free distribution and natal dispersal in female roe deer. Oecologia 103:302–308.

Waser, P. M., and W. T. Jones. 1983. Natal philopatry among solitary mammals. The Quarterly Review of Biology 58:355–390.

Figure legends:

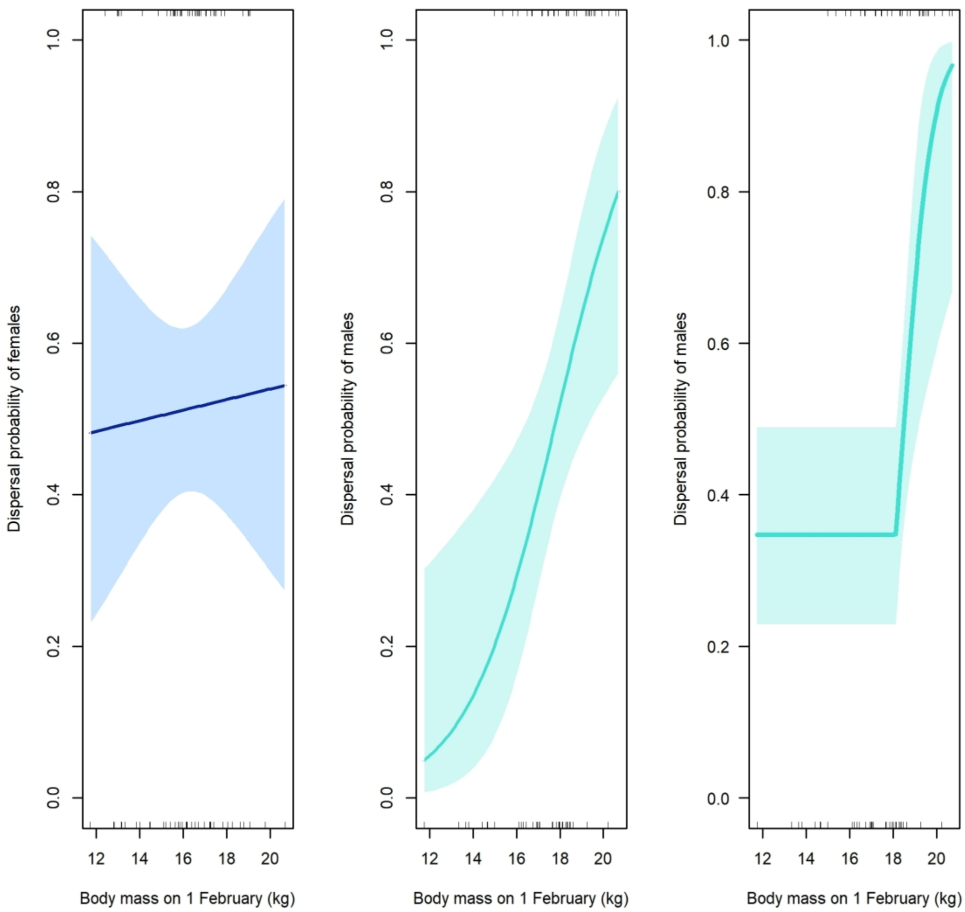
Fig. 1. Dispersal propensity in relation to body mass on 1st February for male and female juveniles in the Aurignac roe deer population (N = 146). The left-hand and middle panels represent the predicted sex-specific relationships derived from the best GLM model, which included the interactive effects of sex and body mass. The right-hand panel represents the predicted relationship for males only based on a threshold model (threshold at 18.1 kg, see text for details).

Fig. 2. Dispersal distance kernels (km) for dispersing male and female juveniles in the Aurignac roe deer population (N = 72).

Fig. 3. Dispersal distance (km) in relation to body mass on 1st 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 blue for males and dark blue for females for visualisation 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 Table S2).

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 1st 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 1st February. For the sex term, the reference category is female.

Response variable	**Parameter**	**Estimate ± s.e.**	**z-value**
a. Dispersal propensity	(Intercept)	-0.40 ± 1.98	-0.202
	Sex (male)	-8.25 ± 3.70	-2.231
	Body mass	0.03 ± 0.12	0.230
	Sex (male) x Body mass	0.46 ± 0.21	2.138
b. Dispersal distance	(Intercept)	-24.121 ± 4.947	-4.875
	Body mass	1.995 ± 0.371	5.376



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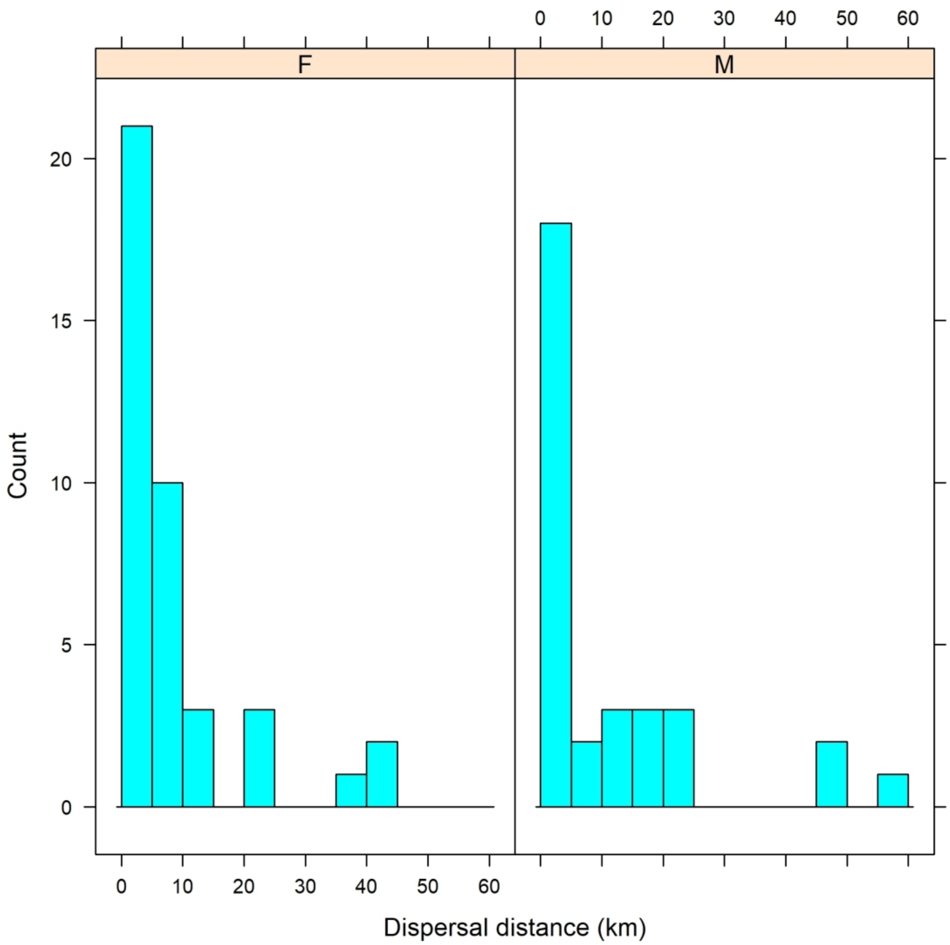

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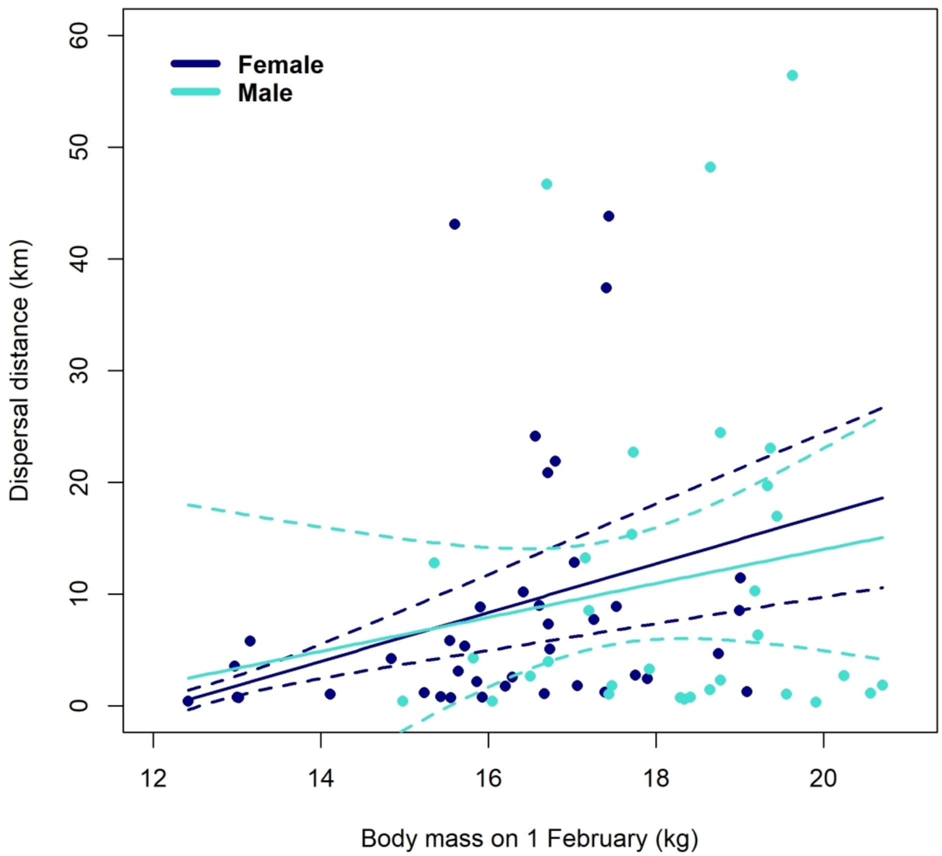

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