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Animal behaviour

Changing motivations during migration: linking movement speed to reproductive status in a migratory large mammal

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A challenge in animal ecology is to link animal movement to demography. In general, reproducing and non-reproducing animals may show different movement patterns. Dramatic changes in reproductive status, such as the loss of an offspring during the course of migration, might also affect movement. Studies linking movement speed to reproductive status require individual monitoring of life-history events and hence are rare. Here, we link movement data from 98 GPS-collared female moose (*Alces alces*) to field observations of reproductive status and calf survival. We show that reproductive females move more quickly during migration than non-reproductive females. Further, the loss of a calf over the course of migration triggered a decrease in speed of the female. This is in contrast to what might be expected for females no longer constrained by an accompanying offspring. The observed patterns demonstrate that females of different reproductive status may have distinct movement patterns, and that the underlying motivation to move may be altered by a change in reproductive status during migration.

1. Introduction

Multiple factors affect animal movement. Information on the underlying drivers can be obtained by studying movements through space and time [1,2]. If an animal behaves optimally, it should move when the costs of staying are outweighed by the benefits of moving to a different area [3,4]. The factors that influence movement can be divided into those related to external environment (food, predation and competition) and internal state (reproductive status, navigational and movement capacity) [5]. The costs and benefits of movement should affect an individual's survival and reproduction and thus demography and population dynamics [6]. Reproduction also entails costs and they should also affect the movement of an individual [7,8].

There are few studies on the impact of female reproductive status on her movement characteristics (except home range sizes). Most studies have tried to estimate parturition time by using movement data [8,9], often collected as speed and direction [10]. The underlying assumption for estimates of parturition time is that the female should remain in a small area during parturition and as long as the offspring is alive and not able to walk long distances. Her care for the relatively immobile and slow-moving offspring will be reflected in significantly lower movement speed [9,11]. When a female, e.g. by an accident, loses her young offspring, these constraints are lifted and her movement rates are expected to return to the pre-calving level [9]. For mammalian females, the demands of giving birth and supporting an offspring may also affect movement [10]. More generally, the movement characteristics of females will be affected by the life history of the species and by environmental constraints and thermoregulatory demands. Taken together, these constraints may influence an individual's decision to either minimize travel time to reach a location or maximize energy by moving slowly and remaining in favourable habitat [11,12].

Here, we examine the movement patterns of migratory adult female moose (*Alces alces*) to test the hypothesis that changes in reproductive status of females over the course of migration may modify their underlying motivation to move. Moose are generally solitary migrators and calves usually follow cows until the end of their first year, after which they separate. If reproductive status affects movement, we expect that, throughout the migratory cycle, reproductive females will move more slowly than non-reproducing ones, and will change direction more often compared to non-reproducing females (to allow their offspring to keep up). On the other hand, it is conceivable that mothers that lose an offspring would move more slowly in order to maximize energy gain in favourable habitat. This condition is commonly encountered by migratory mammals and may counter the assumption that mothers may move slowly when the offspring is alive and faster when the offspring is lost.

2. Methods and data analyses

We use 110 individual, yearly tracks from 98 GPS-collared moose cows from northern Sweden (2003–2012; 63–65° N; electronic supplementary material, figure S1). We selected one location per animal per day (close to 00.00) for 22 tracks of migratory non-reproducing cows, 46 tracks of reproductive cows with surviving calf (in the case of twins—at least one survived) and 42 tracks of unsuccessfully reproductive cows, i.e. which lost their calf during summer as confirmed by our field observations. To compare movement characteristics across these three groups, we calculated the distance, timing and duration of migration for each individual by the net squared displacement (NSD) approach [2]. NSD is a single time-dependent distance statistic which measures the straight-line distances between the starting point and the subsequent locations for the movement path of a given individual. Nonlinear mixed effects models are then fitted to an individual's NSD to determine the movement parameters. Following this approach, we estimated the speed $V_p(T_i) = V(T_i)\cos(\psi(T_i))$ and directionality $V_t(T_i) = V(T_i)\sin(\psi(T_i))$ in time T_i , for the movement phases: spring, summer, autumn and winter [13]. V_p represents persistence velocity, and captures the tendency and magnitude of movement to persist in a given direction (ψ) for relocations i (from 0 to n), while V_t represents turning velocity, and captures the tendency of movement to head in a perpendicular direction in a given time interval. These measures are more versatile than simple speed or turning, as they capture the primary descriptive features of movement 'i.e. speed, directional persistence and variability' together and account for autocorrelation in the data.

Based on tooth wear observed at capture, females ranged in age from 4 to 8 years with an average of 6.05 years [14,15]. The date of calving, reproductive status (non-reproductive, reproductive and unsuccessfully reproductive) and the calf survival were noted through field checks in May, August and November and 'location clusters' of females at likely calving sites. The location clusters were used to infer the approximate locations of the calving sites for later confirmation in the field (see more information in the electronic supplementary material).

For each female, we observed its reproductive status in the field during the year of observation (three levels:

non-reproductive, reproductive and unsuccessfully reproductive), dates (timing of seasonal movement—spring and autumn migration), and average V_p and V_t in each movement phase. To test for significant differences in movement across groups, we used generalized linear mixed models (GLMMs) with reproductive status of the mother (model set 1: non-reproductive—0, reproductive—1 and model set 2: reproductive—0 and unsuccessfully reproductive—1) as the response variable (binary, in two sets of models) and age, litter size (twin or singleton), velocities and turnings of each migratory phase as explanatory variables (with each season for each animal as single data point) and individual ID as the random effect. We made two sets of models: with paired combinations of non-reproductive versus reproductive, and with reproductive versus unsuccessfully reproductive for speed and direction separately. We used Akaike's information criterion (AIC) [16] to select the best model. Analyses were conducted in R v. 2.15.3 [17]. The heterogeneity of movement estimates in time was pooled to seasons.

3. Results

(a) Trends in movements

Owing to small sample size of the dataset ($n = 22$, non-reproductive; 42, reproductive; 46, unsuccessfully reproductive), it was not possible to include all relevant variables and their interactions in the same models, so model runs were selected primarily based on the specific question.

Overall, reproductive females were, as expected, significantly older than non-reproductive females (estimate \pm s.e.: 1.74 ± 0.9 , $p < 0.05$; table 1), but there was no statistically significant effect of mother's age or litter size on calf survival (table 1).

The three categories of females (non-reproductive, reproductive and unsuccessfully reproductive) mainly differ in their duration of migration and speeds (*persistence velocity* V_p), but note the large standard errors (table 2). Non-reproductive females spent a longer time migrating and were slower, both during spring and autumn migrations, whereas reproductive females were faster (tables 1 and 2). However, according to the mixed model results, these differences were only statistically significant during spring (estimate \pm s.e.: 3.7 ± 2.7 , $p < 0.05$; table 1 and electronic supplementary material, table S1). On the other hand, unsuccessful females were significantly faster in spring than reproductive females (44.55 ± 136.7), but moved significantly slower in both summer (-57.2 ± 158.1 , $p < 0.01$) and autumn (-14.24 ± 96.3 , $p < 0.01$; table 1 and electronic supplementary material, table S1). There were no statistically significant differences observed in directionality between groups for different times of the year, as the model with only the intercept was the best model (table 1 and electronic supplementary material, table S1).

4. Discussion

We found that non-reproductive females moved more slowly than the reproductive females during spring, contrary to the expectation that offspring slow down the females [9]. Our results for the comparisons of successful versus unsuccessful mothers also demonstrate this. Successful reproductive females may move more quickly and minimize time in order to arrive at the calving or rutting grounds and winter ranges to ensure

Table 1. GLMMs results for (a) differences in *reproductive status* of females with respect to age; (b) differences in *reproductive success* of females with respect to age and litter size; and differences in (c) *reproductive status* and (d) *success* with respect to speed of moose females. Values in bold and asterisks (*) indicate significant *p*-values. The results of the best model (after AIC model selection, see the electronic supplementary material, table S1) are presented.

fixed effects	estimate	s.e.	random effect	variance	s.d.
(a) reproductive versus non-reproductive (base non-reproductive)					
intercept	-12.15	5.6	animal ID	46.7	6.83
age*	1.74	0.92			
(b) reproductive versus unsuccessfully reproductive (base unsuccessfully reproductive)					
intercept	37.19	53.36	animal ID	1395.3	37.35
age	-5.96	7.22			
intercept	-32.66	53.18	animal ID	1395.3	37.35
litter size	22.18	45.36			
(c) speed-reproductive versus non-reproductive (base non-reproductive)					
intercept	-2.14	2.82	animal ID	115.63	10.75
spring*	3.68	2.74			
(d) speed-reproductive versus unsuccessfully reproductive (base reproductive)					
intercept	22.15	113.66	animal ID	34114	184.7
spring*	44.55	136.97			
autumn*	-14.24	96.3			
summer*	-57.2	158.1			

* $p < 0.05$.

Table 2. Descriptive statistics of the movement characteristics for the three classes of females (mean \pm s.e.) during the migratory periods (spring and autumn) and seasonal ranges (summer and winter). Units: distance travelled annually; speed/persistence velocity ($V_p = V \cos \psi$, km d⁻¹) and directionality ($V_t = V \sin \psi$, km d⁻¹).

	non-reproductive	reproductive	unsuccessfully reproductive
distance (km)	106.7 \pm 10.4	114.9 \pm 3.7	112.6 \pm 4.8
duration spring migration (days)	23.4 \pm 4.0	16.5 \pm 2.3	17.1 \pm 1.6
duration autumn migration (days)	52.7 \pm 10.0	25.2 \pm 5.0	39.3 \pm 11.3
V_p spring migration	1739.2 \pm 198.3	2149.4 \pm 157.8	2019.4 \pm 112.6
V_p summer	307.3 \pm 42.0	311.1 \pm 34.5	513.2 \pm 98.3
V_p autumn migration	1791.0 \pm 207.3	2140.4 \pm 190.8	2282.0 \pm 251.0
V_t spring migration	1757.4 \pm 156.6	1667.7 \pm 148.2	1524.7 \pm 121.5
V_t summer	20.77 \pm 2.5	21.26 \pm 2.8	17.2 \pm 2.5
V_t autumn migration	1402.4 \pm 147.3	1562.4 \pm 140.6	1324.5 \pm 112.5

increased reproductive success and occupy safer areas within the summer and winter ranges to ensure their calf survival.

Many other seasonally migrating ungulates are known to track forage, and in these species differences are observed between the sexes as well as females of different reproductive status [12,17,18]. In a study on migratory mule deer, Monteith *et al.* [12] reported that autumn migrations were more asynchronous across individuals in comparison to spring migrations (when they gave birth), which was attributed to local differences in habitats used by females. In the context of climate change, it has been suggested that natural selection should favour those individuals that are able to adjust their timing of migration so as to enhance nutrient gain [19,20]. As climate warms, animals are expected to depart winter range earlier in spring, and remain on summer ranges for a longer duration in autumn, in order to maximize the access to forage through

reduced intraspecific competition [21] and access forage of more nutritious phenological stage [22]. In our case, it could very well be that the females that lost their offspring tried to maximize nutrient gain by moving more slowly in order to better access more nutrient-rich forage, and possibly also to avoid competition with other females that arrived earlier at winter ranges.

Our measurements of movement at a daily scale may have obscured finer scale patterns in movement tendency. This could be the reason why no differences in directionality during different times of the year were observed. Females that had twins but lost one did not show movement characteristics that were different from those of females whose single calf survived, as shown by the absence of the effect of litter size. Age affected reproductive status (table 1), and age in interaction with environmental variables such as snow and road

density is known to affect moose movements [2]. This could explain why age in isolation did not affect movement speeds and directionality. In addition, most female moose in Sweden are hunted before living a full lifespan, and hence we did not have animals in the data that would be old enough to show an effect of age on movement [23]. It is also important to note that past studies addressing this question have been on gregarious species; how gregariousness affects an individual's decision to migrate is an aspect that has received little attention [8,9,12]. Our study animals are solitary migrators and are possibly less likely to be influenced by other individuals. Further studies on relating the movement of females with different

reproductive status to habitat use may shed more light on the exact tactics adopted by females of gregarious versus non-gregarious migratory species and tease out the influence of sociality on movement [8,24].

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