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Can we use a functional trait to construct a generalized model for ungulate populations?

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Abstract. Ecologists have long desired predictive models that allow inference on population dynamics, where detailed demographic data are unavailable. Integral projection models (IPMs) allow both demographic and phenotypic outcomes at the level of the population to be predicted from the distribution of a functional trait, like body mass. In species where body mass markedly influences demographic rates, as is the rule among mammals, then IPMs provide not only opportunity to assess the population responses to a given environment, but also improve our understanding of the complex interplay between traits and demographic outcomes. Here, we develop a body-mass-based approach to constructing generalized, predictive IPMs for species of ungulates covering a broad range of body size (25–400 kg). Despite our best efforts, we found that a reliable and general, functional, trait-based model for ungulates was unattainable even after accounting for among-species variation in both age at first reproduction and litter size. We attribute this to the diversity of reproductive tactics among similar-sized species of ungulates, and to the interplay between density-dependent and environmental factors that shape demographic parameters independent of mass at the local scale. These processes thus drive population dynamics and cannot be ignored. Environmental context generally matters in population ecology, and our study shows this may be the case for functional traits in vertebrate populations.

Key words: *demography; evolution; integral projection models; life history traits; mammals.*

Introduction

Given the paucity of adequate demographic data for many vertebrates in the wild (Conde et al. 2019), there has long been an interest among ecologists for models that allow simulation of population-level outcomes but only require a minimal amount of data. Population biologists, in particular those working with models structured with age or stage classes, have for some time recognized the possibility of this, and several studies have looked for assessing from minimal demographic data a metric of population growth commonly used in ecology, the *r*-max value (Pianka 1972, Slade et al. 1998). However, even when using the most accurate predictive model based on the concept of life history invariants (Charnov 1993), as proposed by Niel and Lebreton (2005), these approaches require at least reliable estimates of the age at first reproduction and annual adult survival for the focal species. While age at first reproduction has been assessed in a large range of mammals, such information is unfortunately missing for adult survival in most extant vertebrate species (Conde et al. 2019). By invariant here, we refer to the concept of similarity (sensu Stahl 1962) in scaling among life history traits of a given dimension (e.g., age to sexual maturity and longevity for examples of biological times) across species.

Open-access repositories of life history parameters, such as PanTHERIA (Jones 2009) have gone some way toward addressing these missing data. Some previous work has provided data on demographic parameters across species, which may be used as Bayesian priors for example, to parameterize demographic models (McCarthy et al. 2008). Further, a database of animal population matrices (COMADRE database; Salguero-Gomez et al. 2016) provides demographic data for several hundred animal species, which may crudely allow inference on demographic outcomes for species where data are incomplete. These are based on age- or stage-structured matrix population models, and such models have allowed for comparative demographic studies in the past (Hone et al. 2010, Stott et al. 2010, Gamelon et al. 2014), but see Kendall et al. (2019) for widespread

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problems in matrix design. Age- or stage-structured models distribute individuals within a population by discrete age or size classes, even if the structuring trait that determines demographic parameters such as body mass (indeed mass is linked in survival and recruitment in most vertebrates, e.g., Calder 1984) exhibits continuous variation. Such a distribution of heterogeneous individuals by discrete class introduces error, and any attempts to bypass this by increasing the number of classes leads to fewer data and greater sampling error (Ellner and Rees 2006). Where the trait is a model-structuring trait (viz. a functional trait; McGill et al. 2006), defined as a trait that "strongly influences an organismal performance," then the usefulness of stage- or age-structured models is limited.

There are population models that can be structured by a continuous trait, and these provide for inference across species where that trait can be estimated. These models correspond to Integral Projection Models (IPMs), which should not be confounded with Integrated Population Models (Besbeas et al. 2002). IPMs applied here are based on the relationships between a continuous functional trait (such as body mass) and demographic performance (Easterling et al. 2000, Coulson 2012), thereby avoiding discrete classes. IPMs describe the relationship between the functional trait and survival, the functional trait and recruitment, between the changes in the functional trait (across individuals) from time step t to $t + 1$ (growth) and between estimates of the functional trait across recruits born to parents where the functional trait was also observed (inheritance). See Appendix S1 for a schematic of our model. IPMs can be constructed using any type of relationship linking the functional trait to demographic parameters. IPMs can be used to estimate population structure and growth rate, net reproductive rate, and generation time (Coulson et al. 2010, Coulson 2012, Plard et al. 2015*b*, Vindenes and Langangen 2015). Since IPMs may be built on a limited number of functions, e.g., four in the case of vertebrates with an annual life cycle (Plard et al. 2015*b*), then it should be reasonable to assume that if the functional trait is the same among species and if the shape of these functions varies consistently across species, it may just be possible to construct a general, predictive IPM structured by one or a limited number of functional traits.

Functional traits include any morphological, physiological, or behavioral trait of individuals, expressed as a phenotypic trait and shaping the response of individuals to their environment (Diaz et al. 2013). Although there has been recent interest in the role of functional traits in community structure, many studies to date have focused on plant populations (Adler et al. 2014), with little attention on vertebrates. Previous work has focused on the direct influence of environmental changes on demography and very few trait-based demographic analyses have been performed. However, just as there may be a population-level demographic response to a changing environment, changes in trait-based demography are likely.

Thus a general demographic-functional trait model that could be used by biologists to assess the trait responsiveness and demographic outcomes of a species of concern to, say, harvest or shifts in climate would be desirable where data are otherwise unavailable. We aimed to construct such a general, predictive IPM structured with a functional trait to estimate the key quantities that allow assessing population dynamics and life history (i.e., population growth, net reproductive rate, generation time) for any species of ungulate. As body mass is an expectedly fundamental functional trait that influences individual vital rates within a population in most vertebrates (see, e.g., Calder 1984), we used body mass as the functional trait in the present analysis. Our population model also included age structure to account for variation in age of first reproduction. We based our analyses on ungulates because they are ecologically important from both academic and societal viewpoints (Hobbs 1996, Gordon et al. 2004).

Our approach involved three steps. First, we collected detailed demographic and growth data from a low number of long-term longitudinal studies to parameterize the functions, providing associations between mean body mass and mean age-dependent survival, mean age-dependent recruitment, body mass broad-sense inheritance, and change in mass between time steps (see Appendix S1). Then, we built IPMs from these relationships for three species with highly contrasting adult mass that covered most of the mass range observed in ungulates (i.e., 25, 100, and 400 kg). Finally, we compared the outcome of these IPMs with detailed demographic outputs available from individual long-term studies of species corresponding to these size classes, as a form of "truthing" our model.

Methods

We set out to parameterize a predictive IPM for species of ungulates, based on detailed demographic data available from detailed long-term studies. We restricted our study to species from the order of *Artiodactyla*. A step-by-step explanation of model parameterization is provided in Appendix S1.

Integral projection models

IPMs are built as transition matrices, but unlike classic matrix models, demographic parameters are continuous functions of the functional trait (here body mass). The four required functions were determined using regression models with the appropriate distribution (i.e., binomial distribution for survival, Poisson distribution for recruitment, and normal distribution for both growth and inheritance), and describe (1) survival as a function of body mass, (2) recruitment as a function of body mass, (3) body mass growth among all individuals from one year to the next, and (4) the relationship between maternal body mass and that of the recruit

(Easterling et al. 2000). A detailed description of IPMs, mathematical notation, and R code can be sourced from Coulson (2012).

To develop a predictive IPM, for an ungulate of any given body mass, we need to be able to take the mean adult female mass for that species, and from that derive the four functions required to construct an IPM. To do this, we assumed that each of the four functions varied in a predictable manner across species.

For each focal species, we constructed an age-class, post-breeding census, female-based model on an annual time step. The number of age classes was equal to age at first reproduction. Most Artiodactyla females first breed at 3 yr of age or younger. For females breeding at 2 yr old, we used two age classes (newborn and adults). For females breeding at 3 yr old, we included three age classes (newborn, immature, and adult). In species where primiparity is delayed, a larger matrix was built by increasing the number of immature age classes. As an example, the transition matrix of a species with an age at first reproduction at 3 yr old corresponded to

$$\begin{matrix} 0 & 0 & I*R*G*\mathrm{SA} \\ G*\mathrm{SJ} & 0 & 0 \\ 0 & G*\mathrm{SA} & G*\mathrm{SA} \end{matrix}$$

where R is the annual fecundity (measured as the number of daughters born per female aged 1 yr or older), SJ is the juvenile survival (survival from birth to 1 yr of age), and SA is the annual adult survival of females older than 1 yr of age. These three demographic rates also depend on body mass. Thus, two additional rates need to be included in the model: G, which corresponds to the growth linking body mass between two successive years and I, which links body mass of recruits to maternal body mass. We did not account for actuarial senescence, although it is widespread in ungulates (Nussey et al. 2013), and assumed no age-dependent change in survival during adulthood. Next we provide an explanation of how functions were estimated based on a 25 kg species.

Estimation of age at first reproduction and assessment of the recruitment and survival functions

To estimate species-specific age of first reproduction, we updated data from Wootton (1987) linking female adult body mass to age of first reproduction (AFR) in mammals to obtain information on 80 ungulate species. We then fitted an allometric relationship and found a slope of 0.26 (SE = 0.021, $t = 12.576$, $P < 0.001$), close to the value of 0.25 expected for a biological time (Calder 1984)

$$\begin{aligned}&\mathrm{Log}(\mathrm{AFR}) = \\ &-2.120 + 0.262 \times \log(\text{Female adult body mass (g)}).\end{aligned} \tag{1}$$

For our 25-kg IPM species model, we thus predicted an age of first reproduction of 2 yr of age. We built a two age-class post-breeding model: newborn (0–1) and mature individuals (>1) in such a situation.

To assess the age-specific survival function of the IPM, we looked for estimates of juvenile and adult survival from detailed long-term field studies of ungulate populations (see Gaillard et al. 1998, 2000*b*). We found reliable estimates for 21 different species of ungulates for which measures of mean birth mass and mean adult body mass of females were also available. We fitted linear regression models of juvenile survival against birth mass and of adult survival against adult female mass across the 21 species. To obtain relationships, we logit-transformed juvenile and adult survival (so to obtain juvenile and adult life expectancies [Seber 1973] scaling as biological times) and log-transformed birth and adult body mass

$$\mathrm{Log}(\mathrm{SJ}/(1-\mathrm{SJ})) = -0.882 + 0.710 \times \mathrm{Log}(\text{Birth mass(kg)}) \tag{2}$$

$$\begin{aligned}&\mathrm{Log}(\mathrm{SA}/(1-\mathrm{SA})) = 2.145 + 0.0675 \\ &\times \mathrm{Log}(\text{Female adult body mass (kg)}).\end{aligned} \tag{3}$$

The slope was statistically significant for juvenile survival ($t = 3.34$, $P = 0.003$) but not for adult survival ($t = 0.47$, $P = 0.65$). For our 25-kg IPM, we directly used these two equations to parameterize the juvenile and adult survival functions at the population level.

Fecundity was estimated as the number of young born per female per year (accounting for possible twinning), multiplied by a sex ratio of 0.5. Based on the strong relationship between annual fecundity and body mass (Gaillard et al. 2000*a*), we set the fecundity function to increase linearly on a log scale from 0.1 at 75% of the average species-specific adult mass (Servanty et al. 2009) to the average species-specific fecundity when the average species-specific adult mass was reached. Average fecundity for a given species was obtained from the interspecific allometric relationship provided by Allaine et al. (1987) from 48 species of *Artiodactyla*.

For our 25-kg IPM, we used the predicted average fecundity from Allaine et al. (1987) for a 25-kg species: 1.36 young per female. Then we found the intercept and the slope of the linear function linking fecundity to body mass that can be drawn between these two points: 0.1 fecundity at 18.75 kg and 1.36 young at 25 kg, leading to the function $R = -3.680 + 0.202 \times$ kg body mass.

Parameter estimation of growth and inheritance

The inheritance function describes birth mass in relation to maternal body mass (see Coulson 2012 for discussion on the distinction between *inheritance* and *heritability*). The inheritance function has been modeled using a normal distribution with a variable mean and a fixed variance. The variance was a priori fixed at 1 to get realistic distributions of newborn size. We perturbed this variance value to check whether this fixed value had a

marked effect on demographic outcomes (Appendix S1: Fig. S6). The mean of the inheritance function predicting newborn body mass from maternal body mass was obtained from the allometric relationship established by Robbins and Robbins (1979) across 42 species of ungulates (see Appendix S1). Because inheritance functions have been well fit to the existing data for IPMs on ungulates (Traill et al. 2014, Plard et al. 2015*b*), we used linear regressions and showed that the allometric relationship of Robbins and Robbins (1979) could be well approximated using a piecewise linear regressions with a body mass close to 70 kg as a threshold value (see Appendix S1). Using a female adult mass of 70 kg as a threshold, we obtained the following equations.

For species with females lighter than 70 kg, such as for our 25-kg IPM case study

$$\text{Birth Mass (kg)} = 0.531 + 0.084 \times \text{Adult Female Mass (kg)}. \quad (4)$$

For species with females heavier than 70 kg

$$\text{Birth Mass (kg)} = 3.531 + 0.054 \times \text{Adult Female Mass (kg)}. \quad (5)$$

The growth function describes the probability to reach a body mass at time $t + 1$ given a body mass at time t. The growth function was the same for all age classes at it already accounts for the decrease of individual growth rate as individuals grow from birth onward, which is typical of growth patterns in precocial mammals such as ungulates (Gaillard et al. 1997). As with the inheritance function, it was modeled with a normal distribution with variable mean and a fixed variance. The variance was fixed to 5 to get realistic distributions of animals (and we carried out an elasticity analysis to check the lack of effect of variance). Typically for the mean of the growth function, data available from individual-based studies track each individual through time, allowing the estimation of growth by regressing body mass at time $t + 1$ on body mass at time t for age classes of interest. As we did not have repeated measures across individuals, we used body mass at three key life stages (newborn, yearling, and adult stage) to get two measures of mass changes between t and $t + 1$ (see Appendix S1). As the mean of the growth function, we found the intercept and the slope of the linear function that cross two points: the first point linked birth mass and yearling mass. The second point was the stationary point linking adult body mass to adult body mass. Indeed, all ungulates are deterministic growers that reach an asymptotic mass (up to an age of onset of senescence when body mass starts to decrease with increasing age; Nussey et al. 2011), which does not vary over time other than stochastic variation around a mean. Note that senescence in mass should not be taken into account at the population level of our analyses. Indeed, the negative influence of senescence in mass detected from individual trajectories is cancelled out by the positive influence of selective disappearance that occurs at the population level so that, in a given year, prime-aged adults and oldest individuals display remarkably similar body mass (Nussey et al. 2008). For estimating birth mass, we used the piecewise regression of mean birth mass on mean maternal mass (see Eqs. 3 and 4). To obtain yearling mass, we used the relationship between yearling and adult mass displayed by Toigo et al. (2007) from data collected on nine species of Artiodactyla. Assuming that ungulates reach about the same the proportion of adult mass at 1 yr of age (which was observed in eight out of the nine species included in Toigo et al. 2007), we retained the mean proportion observed (75%) for all species.

To build the growth function for body mass (BM) for our 25-kg example, for instance, we found the slope and the intercept of the linear relationship crossing these two points: 2.63 kg (birth mass) against 18.75 kg (yearling mass = 75% × 25) and 25 kg against 25 kg (adult mass): $\text{BM}_{t+1} = 18.015 + 0.279 \times \text{BM}_t$.

Generalized integral projection model

As we detailed for a 25-kg-species case study, based on the mean adult body mass of the focal species, the four IPM functions for this species are determined by the regression parameters (intercept and slope) as estimated above. By including these functions in an IPM, we aimed to predict demographic and evolutionary outcomes for any ungulate species, irrespective of its mating tactic, diet, and social structure. Thus, we selected three surrogate herbivores of differing body mass, crudely representing small- (25 kg), medium- (100 kg), and large-sized (400 kg) species, which covers the whole range (on an allometric scale) of extent ungulates except the few tiny (<10 kg) and mega-herbivore (>1,000 kg) species. An IPM was constructed for each of these three herbivorous ungulates within the R language (R Development Core Team 2019). For each species, we estimated lambda, R_0, generation time, average age-specific body mass, age-class-specific survival, and fecundity at population equilibrium and compared the estimated values to values obtained from detailed long-term individual data on four populations of roe deer in France (about 25 kg; Gaillard et al. 2013), Pyrenean chamois (*Rupicapra pyrenaica*) in France, which are about 25 kg and do not twin, (Crampe et al. 2006), red deer (*Cervus elaphus*) on the Isle of Rum (Benton et al. 1995), and moose (*Alces alces*) in Sweden (Ericsson et al. 2001). As a further comparison to understand if fecundity and age at first reproduction were responsible for the lack of fit between predicted parameters from the generalized IPM and observed parameters, we ran four supplemental population-specific IPMs (one for each population). These four IPMs differ from the generalized IPMs as we set the age of first reproduction and the fecundity function to fixed

values corresponding to the observed values in the four populations.

Results

Size-dependent demography across species of ungulates

Age at first reproduction was delayed for heavier species from 2 yr of age for small and medium ungulates to 3 or 4 yr of age in large ungulates. Heavier species displayed higher survival in both juvenile and adult stages (Fig. 1). However, the large variation in body mass did not appear to have a substantial effect on mean age-specific survival across ungulates, especially in adults. The average adult survival only slightly increased with adult mass: 0.91 for small species, 0.92 for medium-sized species, and 0.93 for large species. The influence of species' size was more pronounced on juvenile survival. While juvenile survival was only 0.44 in small species, it increased to reach 0.66 in medium-sized species and 0.80 in large species. Likewise, while the average fecundity decreased with increasing species size, the response was only weak. While a mature female in a small species gave birth to 0.50 daughters per year, a mature female in a medium-sized species and in a large species produced 0.39 and 0.32 daughters per year, respectively.

As expected, the mean birth mass and mean adult female body mass distributions were markedly different among species with contrasting body size. Birth mass averaged 2.7, 8.7, and 25.0 kg in small, medium, and large species, respectively. The respective average adult sizes (including immature and mature individuals) were 23.6, 93.8, and 378.0 kg.

Simulations for small- to large-sized species provided realistic demographic output, but the contrast among species markedly different in size was much less than expected. The population growth at population equilibrium (λ) was remarkably similar among scenarios (1.11 for a 25-kg species of ungulates, 1.14 for a 100-kg species, and 1.12 for a 400-kg species), suggesting that population growth is quite fixed (around 1.12) among species of ungulates, irrespective of their size. Likewise, although generation time (calculated from the net reproductive rate and from the population growth rate) displayed the expected increase from medium to large species, the magnitude of the difference was weak (9.96 for a 25-kg species, 9.92 for a 100-kg species, and 11.72 for a 400-kg species). Last, R_0, the net reproductive rate slightly increased with species mass from small to medium species, being 2.87 for a 25-kg species, 3.73 for a 100-kg species, and 3.73 for a 400-kg species.

Assessing the accuracy of size demography derived from the generalized IPM for ungulates

The observed λ values for roe deer, a 24-kg species, intensively monitored in two populations in France were 1.19 and 1.15 (Gaillard et al. 2013), a bit higher than that predicted from our generalized IPM for a 25-kg ungulate: 1.11. Adult survival estimates for roe deer is 0.92 (Choquet et al. 2011), not too dissimilar to estimate from the generalized IPM 0.91. However, survival is 0.65 before 8 months of age, and up to 0.85 after 8 months higher than expected from our IPM: 0.44. Individual heterogeneity in juvenile and adult survival as well as in other demographic functions was poorly represented by the demographic functions from the generalized model (Fig. 1). Our general IPM predicted mean birth mass for a 25-kg herbivore to be 2.7 kg, substantially larger than estimated for this population: 1.593 kg (Plard et al. 2015*c*) and adult mass to be 23.6 kg, similar to observed adult mass. On the other hand, recruitment at birth was markedly underestimated because most roe deer females produce twins (Gaillard et al. 2013), leading generation time to be substantially overestimated; 5 yr in Plard et al. (2015*a*) instead of almost 10 with our generalized IPM. Using the population-specific IPM with fixed observed fecundity and age at first reproduction, we found a generation time of 7.38, still higher but closer to the one in this population, showing some remaining discrepancies between the dynamics of the roe deer population and the generalized IPM, particularly in juvenile survival (0.43 in the IPM vs. 0.65 in the population).

We further compared the output of our small-species-generalized IPM to parameters obtained in a population of Pyrenean chamois. Adult survival and body mass of Pyrenean chamois were similar to roe deer and to predictions from the generalized 25-kg IPM. However, as Pyrenean chamois do not twin, recruitment rate in this population (0.414; Crampe et al. 2006) was close to the one predicted from the generalized 25-kg IPM: 0.50 (and 0.457 from the population-specific IPM). Generation time was slightly higher but also comparable between the generalized IPM 9.96 and the value previously reported for this population: 8.65. Nevertheless, lambda for Pyrenean chamois was 1.04, substantially lower than for our generalized 25-kg IPM: 1.11. Indeed, the age of first reproduction is 3 yr in this population instead of 2 as predicted from the generalized IPM. Accounting for observed age at first reproduction, lambda from our population-specific IPM was 1.07, closer to that observed in the Pyrenean chamois population.

Red deer females on Rum Island, which have been intensively monitored for several decades, weigh about 100 kg. Age-class survival rates obtained were very close to those estimated on Rum: 0.61 for juvenile survival and a maximum of 0.95 for prime-age-females (Benton et al. 1995) vs. 0.66 and 0.92 in the present work. Our general model predicted mean birth mass for a 100-kg herbivore to be 8.7 kg, again higher than the 6.5 kg previously found in this population (Stopher et al. 2014). The productivity of the Rum population, however, was much lower than that estimated from the IPM. While the IPM indicated that each red deer female of 2 yr of age and older should give birth to about 0.39 newborn

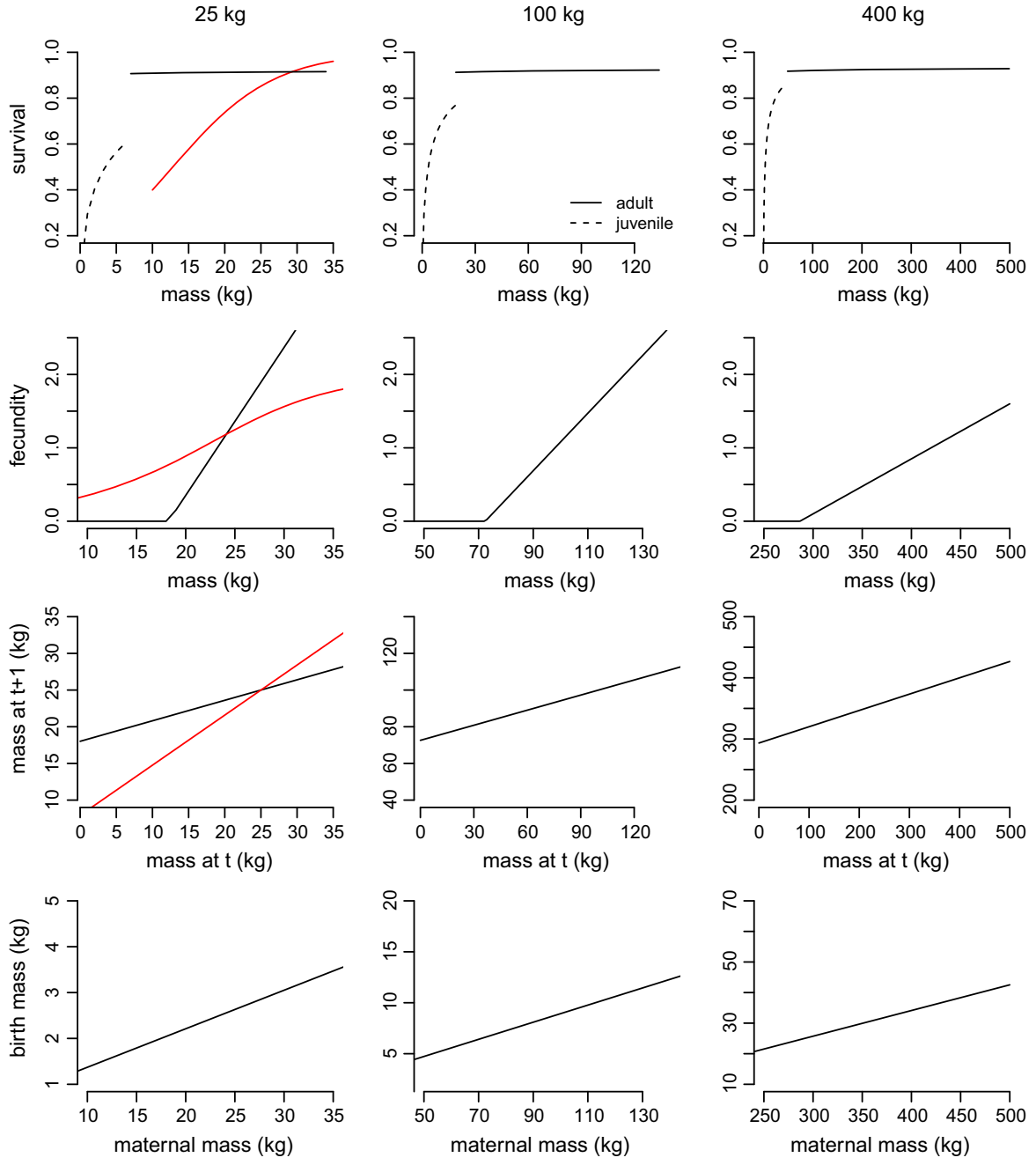


FIG. 1. Functions of the integral projection model (IPM) predicted for the small- (25 kg), medium- (100 kg), and large-sized (400 kg) species. Red lines show functions of a previously published IPM estimated from long-term individual data on a population of roe deer in Trois-Fontaines, France (about 25 kg; Plard et al. 2015). As offspring entered in the model at 8 months old in this previous paper (i.e., we used a pre-breeding census model), we cannot display and compare the predicted juvenile survival and inheritance functions with the one estimated from Plard et al. (2015). Note that the comparative projections of the roe deer IPM and those of our global model need to be interpreted with some caution, as our global IPM is based on interspecific relationships and cannot account for intraspecific variation within and among populations. In the third row, mass is compared at time t and time $t + 1$.

females, field estimates on Rum show that females only give birth from 3 yr of age onward, producing an average of about 0.25 newborn females. As a result, the population growth rate (1.14) obtained from the IPM was much higher than that reported on Rum (1.04 calculated from demographic data reported in Benton et al.

[1995]). Using our population-specific IPM with a fixed fecundity of 1 and age at first reproduction of 3, we found a λ of 1.05, closer to that reported in the population. However, the generalized IPM outcome might fit the demography of red deer from more productive populations (Bonenfant et al. 2002).

Last, moose intensively studied in Sweden (Ericsson et al. 2001) provided field estimates for a species of ungulates close to 400 kg. In these populations, adult female mortality was especially low (when the influence of hunting was accounted for) and adult survival matched the mean survival close to 0.93 reported from the IPM (Gaillard 2007). However, juvenile survival was lower in the Swedish population (0.64) than the value obtained from the IPM (0.80). Again adult body mass was close to observed in the population but birth body mass was overestimated (24.98 kg for a 400 kg herbivore vs. about 14 kg in the population). The more pronounced difference was again about recruitment at birth. While the IPM estimate was 0.32 female per female 3 yr of age and older, the average yearly recruitment between 3 and 14 yr of age varied between 0.5 and 0.75 in relation to the high proportion of females that twinned. As a result, the generation time issued from the IPM was larger than any values reported from the field in moose populations (11.72 yr in the present work vs. a range from 4.57 to 10.66, median of 6.5, in the review by Gaillard [2007]). Again, using our population-specific IPM, we found a generation time closer but still higher (10.76) to the one of this population, juvenile survival remaining overestimated.

Discussion

Our best attempt to construct a generalized, functional-trait-based IPM, allowing one to predict the demographic rates and the distribution of a functional trait for an ungulate population where data are minimal, produced mixed findings. Mixed because, while our model output based on mean demographic rates were reasonably possible, we would not recommend such a model for decision making; principally because our IPMs were unrealistic, especially in terms of recruitment (reproduction and juvenile survival) and generation time. The failure to provide a robust model based on one functional trait, even as structuring population dynamics as body mass in ungulates and for a relatively well-studied taxonomic group, has some consequences. To date, much of the recent literature about insight provided through functional traits has pertained to plants, and our work indicates that the use of a functional trait frequently measured in vertebrates (such as body mass) may not be easily generalized. We used a mathematical framework to explicitly link one functional trait to demographic outcomes across a well-studied taxonomic group, and we failed in our attempt to build a realistic generalized model.

Our findings likely demonstrate that the environmental context matters, viz. localized density-dependent and environmental effects. In particular, the absence of consideration of density dependence when building the IPMs might partly account for our finding of an almost equal population growth rate among small, medium, and large species. Density dependence is a main driver in population dynamics (Coulson et al. 2001) and is the rule rather than the exception in ungulate populations (see Bonenfant et al. 2009). Population density should therefore be known for a population to build correctly a population model and predict reliably its dynamics. Environmental factors generally determine population-level response in ungulates, and further to abiotic factors is the critical role that age and sex structure play in population dynamics (Coulson et al. 2001). We cannot show this with our model, but suggest these factors may be behind the lack of predictive power of our generalized model, in particular for the recruitment rate. It may also be that perhaps another functional trait may better explain demographic outcomes across this taxonomic group. For instance, variation in birth timing in relation to plant phenology is known to strongly influence ungulate population dynamics (Plard et al. 2014) and adding birth dates to mass might improve the ability of a general IPM for ungulates.

Adult survival is generally high in all ungulate species studied so far (Gaillard and Yoccoz 2003), and unsurprisingly, the survival functions of the IPM provided quite accurate predictions in all cases. Nevertheless, the survival functions from the generalized IPM were unable to account for the heterogeneity in survival of individuals of different mass within a population. It appears that much of the deviation observed in the demographic outputs between the IPM and population-specific demographic parameters estimated from intensive field studies, was related to a poor assessment of reproduction and juvenile survival. While body mass plays a fundamental role to set the onset of reproduction, it does not allow accounting for species-specific reproductive tactics. At a given mass, females in some species can reproduce at 1 yr of age (e.g., Soay sheep), whereas others do not (e.g., roe deer). Moreover, the ability to twin is not well predicted by the species' body mass. Thus, while females in the relatively small roe deer commonly produce twins (Plard et al. 2015*b*), Pyrenean chamois and similar-sized gazelles or duikers do not (Kingdon 2013). Likewise, while females of medium-sized white-tailed deer commonly produce twins (Jones et al. 2010), those of similar-sized mountain ungulates do not (Geist 1971). Last, while females of most ungulates usually produce a single offspring (Kingdon 2013), female moose, the largest species of ungulates in the Holarctic range, often twin at a high rate (Gaillard 2007).

Thus, we recommend adding as much information as known on a focal species or population. But even when accounting for observed mean age at first reproduction and litter size in our population-specific IPM, the estimated demographic rates were still different from the ones observed in wild populations, while closer than

estimated from our generalized IPM. The high variation in juvenile survival, which is driven by the interplay between female attributes and environmental contexts independently of the species size, makes reliable predictions of recruitment at birth almost impossible for a given species in a given context.

Juvenile survival, usually defined as survival between birth and 1 yr of age, indeed varies a lot within populations of ungulates (with an average CV of 0.346 across 43 populations; Gaillard et al. 2000*b*), and generally accounts for most observed variation in recruitment. Some a priori knowledge on the level of juvenile mortality in the focal population is thus needed to assess reliably the demography of ungulates. Unfortunately, getting this information is far from an easy task because the level of juvenile mortality is shaped by the interplay among a large number of ecological factors. While an environmental context defined by high predation risk, high population density, harsh weather conditions around birth, and poor food resources would reliably predict a low juvenile survival (say 0.25 or less) and the context with opposite features a high juvenile survival (say 0.75 or more) independently of species size, the multiple potential combinations among these population characteristics that are likely to vary over time, especially when considering a long period, will prevent any reliable prediction of juvenile survival.

The lack of reliable species-specific prediction of reproductive tactics and recruitment prevents us from recommending our model as a basis for decision making (see Bunnefeld and Keane 2014). However, our modeling is useful for targeted field data collection for an ungulate of a given mean adult mass. While adult survival, the most potentially influential variable for varying population growth in long-lived species such as ungulates, was the first priority of past studies, we found that our present knowledge of adult survival among ungulates allows reliable predictions over the whole range of species size, simply because this parameter is remarkably similar across the size range of ungulates (as shown by the lack of allometric relationship for this trait we report here). On the other hand, the absence of general fecundity patterns among ungulates strongly limits the relevance of our general IPMs for practical use. Future research effort should thus target recruitment parameters, which are also those most likely to fine tune the demography of a given species in a specific environmental context (Gaillard et al. 2000*a*).

Individuals of different age, size, and sex within a population also differ in demographic performance, and this individual variation has to be included in the IPM to provide realistic outcomes. We urge ecologists to determine and address the role of life history traits, such as recruitment and environmental variation on population demography to guide management. Population dynamics are typically complex and transient (Benton et al. 2006), and not all ungulates are equal, even at a given size.

In closing, we recommend that *tailored* models, based on long-term, preferably individual-based data (see Clutton-Brock and Sheldon 2010), including functional trait data, are required to deconstruct the complex, interacting factors that drive demography of ungulates. Attempts, such as ours to build general predictive models are useful exercises, but we recommend that inference across vertebrate taxonomic groups, by a functional trait, be treated with some caution.

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