



COMMENT

Age structure matters for Alpine ibex population dynamics: comment on Lima & Berryman (2006)

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Very much progress has been achieved in recent years with respect to understanding vertebrate population dynamics. We know today much more about the importance of climate, population density, and resource abundance in determining population growth rate. Although the conceptual ideas are often not new (Elton 1942), a combination of high-quality data sets (often based on individually marked animals), better statistical methods (especially capture-mark-recapture and time-series statistical models), and demographic tools (such as matrix models and sensitivity analyses), have played an important role in recent advances (Caswell & Fujiwara 2004).

Large vertebrates are characterized by high and nearly constant adult survival and by low and quite variable recruitment (Gaillard et al. 1998). Therefore their populations are strongly age-structured, with different age classes showing different sensitivity to e.g. climate, and therefore fluctuating in their relative abundance. A large number of empirical and theoretical studies have now shown that it is necessary to take into account age structure when e.g. estimating density dependence (Lande et al. 2002, Festa-Bianchet et al. 2003), identifying important parameters for management and conservation (Caswell 2000, Eberhardt 2002, Gaillard & Yoccoz 2003) and predicting future population size (Coulson et al. 2001). Most relevant here is the fact that interactions between age structure and stochastic recruitment lead to trends that are difficult to separate from e.g. climatic forcing (Bjørnstad et al. 2004). Such trends are not observed in unstructured models (i.e. those without age structure).

Ibex *Capra ibex* exhibit the typical survival pattern of large vertebrates with a very high adult survival

(Gaillard et al. 2000). However, survival of yearling and males is much higher than in other large herbivores (Toïgo et al. 1997). Age structure of ibex populations may therefore be characterized by a high proportion of old animals, particularly so when populations are stable or declining. As survival and reproduction of old individuals is lower and more sensitive to environmental factors than those of prime-age individuals (Gaillard et al. 2000), the impact of e.g. climate on population dynamics will depend on age structure (Coulson et al. 2001). This dependence will be particularly strong in ibex populations compared to other large herbivores. By ignoring age structure, Lima & Berryman (2006, this issue) indeed might have made what they refer to as 'misleading, or even dangerous, [...] *a priori* assumptions'.

Lima & Berryman (2006) instead focus on one specific aspect of the study by Jacobson et al. (2004): the use of a threshold model as an approximation to the modelling of interaction between snow and density. We entirely agree that models based on e.g. splines represent a great development in statistical modelling (Wood 2006), and we have used them in various contexts (e.g. Mysterud et al. 2001, Weladji et al. 2006). Clearly the flexibility of additive models represents an improvement over simple applications of linear models. Note that the final model retained by Lima & Berryman (2006) did not include the main effects of density and snow depth, while it did retain the interaction between them. This may be fine from a statistical curve-fitting point of view, but corresponds to an assumption of no effect of density when snow depth is 0 (and no impact of snow when density is 0), which is out of the range of observed data and does not make

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much sense biologically. This problem of not including main effects while retaining interaction terms is not specific to population dynamics models, and is criticized (for example) in general terms by Nelder (1992). Excluding terms from a model on statistical grounds without assessing how this translates in terms of biological assumptions cannot be good advice.

All models are approximations and their usefulness should be judged by their ability to correctly reveal the important features in the data, and in providing robust predictions. Both the threshold model and the additive model reveal the same strong nonlinear effect of density as a function of snow depth, an effect somewhat apparent also in the ibex population of the Swiss National Park studied by Sæther et al. (2002, their Fig. 4). Both fail in explaining the stabilization of population size in recent years. Lima & Berryman (2006) invoked a possible competition with the sympatric chamois to account for such a discrepancy. This is likely to remain speculative as the reliability of chamois counts is low (as discussed in Loison et al. 2006). An alternative and more parsimonious explanation is that the ibex populations showed an apparent delayed density dependence due to the interaction between age structure and climatic effects (Lande et al. 2002, Bjørnstad et al. 2004). How much can be learned from modelling will depend on the model structure and of the error/uncertainty inherent in the data. Being based on total population size and assuming that the counts are exact, Lima & Berryman's (2006) models ignore age structure and measurement error, and are unlikely to provide an ecological explanation for the observed pattern of interaction between climate and density (see also Bjørnstad et al. 2004).

In our view, further progress will be accomplished by combining what we have learned using demographic analyses with explicit consideration of ecological mechanisms at the individual level. This will require better data sets, especially replicated long-term studies of individually marked animals together with a better understanding of which climate parameters affect reproduction and survival and their actual measurement in the field. Randin et al. (2006) have shown that generalized linear models may provide more robust predictions on independent replicated data sets than additive models, even if the fit or prediction criteria assessed on the original data was better for the latter. Such replication is badly needed when studying the effects of climate on population dynamics if we are to develop robust predictive tools. Further progress will also require better statistical and mathematical models, in order to combine our knowledge of the demographic structure of populations with hypotheses regarding ecological effects on demographic parameters. Statistical modelling will also allow for the correc-

tion of bias when estimating density dependence due to measurement error in e.g. population size estimates (Stenseth et al. 2003). These are challenging issues, but recent works are quite promising (Besbeas et al. 2005), and some already include the flexibility of additive modelling (Nisbet et al. 2004, Speirs et al. 2005).

Lima & Berryman (2006) address the important issue of how to better describe the emergent structure of population time series, and how climate might affect it. Our opinion is that a more promising approach is to start from basic principles, i.e. demography and our knowledge of ecological mechanisms, and to assess if the resulting structure fits with the data—a bottom-up approach to population dynamics. This does not mean that unstructured models do not have an important role to play in ecology (e.g. Hastings 2005), but that in the case of populations with strongly age-structured dynamics, they are likely to lead to a misleading picture of climatic effects.

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