The ghost fraction of populations: a taxon-dependent problem

J. J. Negro

Estación Biológica de Doñana (CSIC), Avda. Americo Vespucio s/n, Sevilla, Spain

Correspondence Juan José Negro, Estación Biológica de Doñana (CSIC), Avda. Americo Vespucio s/n, 41092 Sevilla, Spain. Email: negro@ebd.csic.es

population sizes or modelling population Estimating dynamics for species with deferred maturity, and thus different age classes, may be challenging if individuals of all age groups do not coexist in space and time. The problem is particularly acute for those populations in which the nonbreeding fraction disperse away from its natal grounds and does not hold permanent territories elsewhere (e.g. Cadahia, Urios & Negro, 2005). This is exactly the model reported in Katzner et al. (2011). Eastern imperial eagles and whitetailed eagles are large territorial raptors. Adults hold and fiercely defend breeding territories in the spring and summer, whereas immature birds wander around for several years, before getting the chance to fill a vacancy in one of the historical territories. This strategy, that repeats itself in most other raptor populations (Newton, 1979), means that breeding adults are relatively easy to survey after just a few years invested in locating nest-sites, whereas non-attached immature individuals are typically hard to monitor.

And whole age classes difficult to survey lead to inaccurate estimates of survival rates needed to feed either population models and/or population viability analyses. Even if the population growth rate (1) is generally less sensitive to variation in the survival of individuals belonging to the younger age classes than it is to changes in survival rates in the adult fraction of the population (Hiraldo et al., 1996; Biek et al., 2002), a gross underestimation of the juvenile class, such as in Katzner et al. (2011) for eagles, definitely affects model outputs.

But, leaving aside the extended problem of surveying animal (or even plant) populations inhabiting remote areas or having secretive habits, the biases imposed by just a difficult-to-estimate fraction of a given population seems to be restricted to certain taxa. Not surprisingly, the example chosen by Katzner et al. (2011) is a bird. First of all, birds may live long lives and deferred maturity, as well as iteroparity, is frequent in the avian class. Considering the remaining vertebrates, structured populations may also be common. However, the ability to fly confers birds a

dispersing potential practically unparalleled in the remaining vertebrate taxa (with notorious exceptions including, e.g. sea turtles, eels and other sea creatures). For instance, immature Egyptian vultures Neophron percnopterus stay in Africa for 2-3 years before returning to their natal sites in the Western Palearctic to attempt breeding for the first time (Grande et al., 2009). This would not happen in an agestructure primate group, where adults, immatures and infants coexist as members of the same social unit in a restricted area. In monkeys, zebras, gazelles or elephants, for that matter, if you are able to survey adults, you may also survey the remaining age classes. It can be argued that in some mammal populations, for example red deer Cervus elaphus or wild boar Sus scrofa, adult males stay away from the females and juveniles for most of the year. This is true, but surveys can easily be adapted to these peculiarities, as in carrying out the surveys in the season when males and females stay together for mating.

Therefore, species in which it is possible to overlook the presence of a fraction of the population important enough as to influence population estimates and projections share this general profile: (i) deferred maturity; (ii) high dispersal capabilities; (iii) long lifespans. This portraits the average apical predator, be it a falconiform (i.e. diurnal raptors) a strigiform (owl), the pelagic procellariforms (petrels) or, changing taxon, the jellyfish-eating leatherback turtles Dermochelys coriacea, or even the amphibians, for which there is scant demographic information (Biek et al., 2002), even though many populations are experiencing catastrophic declines worldwide.

Birds of prey, even if raptor biologist Ian Newton (1979) stated that their study had contributed little to mainstream ecology, have become significant models for population dynamics research in vertebrates in recent years (e.g. Kruger, Liversidge & Lindstrom, 2002). Raptor are iconic species, many of them having endangered populations, and have become the flagship of species-oriented conservation ever since the peregrine falcon Falco peregrinus was saved

from near extinction after the DDT crisis in the 1970s in North America. Raptor population modelling has also been relatively straightforward as the adult fraction is generally very visible and easy to survey, including direct counts at notorious migration flyways such as the Straits of Gibraltar in the Iberian peninsula, Eilat in Israel or Veracruz in Mexico. Similarly, the potential recruitment of populations via estimating clutch size, hatching success and fledgling success is at hand, by monitoring a sufficient sample of nest sites.

The only shadow in this seemingly success story of raptor monitoring is how to estimate survival of the immature individuals. As it was known that adults held territories for long years and populations remained remarkably stable if undisturbed, it was tempting to say that pre-adult mortality was exceedingly large in raptors (ranging from 60 to 90% of the cohort annually depending on the studies). This picture started to change, first thanks to Newton's (1986) long-term study on the Sparrowhawk Accipiter nisus, and more flatly when Kenward et al. (2000) fitted radiotags on large numbers of common buzzards Buteo buteo and were able to demonstrate the existence of a previously overlooked floating population composed of large numbers of nonterritorial individuals. These individuals would become breeders as soon as a vacancy was available in an otherwise saturated population. In addition, Kenward et al. (2000) suggested that previous studies based on band recoveries or insufficient radio-tags just revealed the tip of the iceberg, in the sense that many survivors remained unaccounted for.

Katzner et al.'s eagles and Kenward et al.'s buzzards have in common unexpectedly large floating populations that may explain why raptor populations tend to respond so rapidly to protection and management (Negro, Sarasola & Barclay, 2007). As soon as conditions improve and populations are able to expand its range to reclaimed safe areas, populations increase at fast pace. A good example is again provided by the eastern imperial eagle, but this time in Hungary, thousands of kilometers to the West from Katzner et al.'s eagles in Kazakhastan. The Hungarian eagle's population has experienced a recent range expansion from mountainous forests to lowland agricultural areas, and it has consistently increased 10% per year in the last decade (Horvath et al., in press). Does this have anything to do with the immature birds enjoying higher survival rates and finding breeding opportunities in areas where they begin to be tolerated after decades of persecution?

References

- Biek, R., Funk, W.C., Maxell, B.A. & Mills, L.S. (2002). What is missing in amphibian decline research: insights from ecological sensitivity analysis. Conserv. Biol. 16, 728–734.
- Cadahia, L., Urios, V. & Negro, J.J. (2005). Survival and movements of satellite-tracked Bonelli's Eagles Hieraaetus fasciatus during their first winter. Ibis 147, 415–419.
- Grande, J.M., Serrano, D., Tavecchia, G., Carrete, M., Ceballos, O., Diaz-Delgado, R., Tella, J.L. & Donazar, J.A. (2009). Survival in a long-lived territorial migrant: effects of life-history traits and ecological conditions in wintering and breeding areas. Oikos 118, 580–590.
- Hiraldo, F., Negro, J.J., Donazar, J.A. & Gaona, P. (1996). A demographic model for a population of the endangered lesser kestrel in southern Spain. J. Appl. Ecol. 33, 1085–1093.
- Horvath, M., Demeter, I., Fater, I., Firmanszky, G., Kleszo, A., Kovacs, A., Szitta, T., Toth, I., Zalai, T. & Bagyura, J. Population dynamics of the imperial eagle (Aquila heliaca) in Hungary between 2001 and 2009. : Acta Zool. Bulg. (in press).
- Katzner, T.E., Ivy, J.A.R., Bragin, E.A., Milner-Gulland, E.J. & DeWoody, J.A. (2011). Conservation implications of inaccurate estimation of cryptic population size. Anim. Conserv. 14, 328–332.
- Kenward, R.E., Walls, S.S., Hodder, K.H., Pahkala, M., Freeman, S.N. & Simpson, V.R. (2000). The prevalence of non-breeders in raptor populations: evidence from rings, radio-tags and transeat surveys. Oikos 91, 271–279.
- Kruger, O., Liversidge, R. & Lindstrom, J. (2002). Statistical modelling of the population dynamics of a raptor community in a semi-desert environment. J. Anim. Ecol. 71, 603–613.
- Negro, J.J., Sarasola, J.H. & Barclay, J.H. (2007). Augmenting wild populations and food resources. In Raptor research and management techniques: 401–410. Bird, D. & Bildstein, K. (Eds) Surrey: Hancock House Publishers.
- Newton, I. (1979). Population ecology of raptors. Berkhamsted: T. & A. D. Poyser.
- Newton, I. (1986). The Sparrowhawk. Calton: T. & A.D. Poyser.