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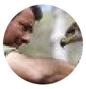

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FORUM

Density dependence hypotheses and the distribution of fecundity

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Summary

1. Beja & Palma (2008, *Journal of Animal Ecology*, **77**, doi: 10.1111/j.1365-2656.2007.01312.x) attempt to provide a critical analysis of the effectiveness and limitations of a previously published method (Ferrer *et al*. 2006, *Journal of Animal Ecology*, **75**, 111–117.) to discriminate between Habitat Heterogeneity Hypothesis and the Individual Adjustment Hypothesis using real data from a Bonelli's eagle *Hieraaetus fasciatus* population.

2. They conclude that significant and strong correlations between mean and CV or skewness are expected under a biologically plausible assumption about brood size distribution, and that the two hypotheses cannot therefore be distinguished.

3. A major concern we have with their paper centres on this biologically plausible brood-size distribution. They used the same quasi-Poisson distribution of brood sizes (typical for a saturate population under Habitat Heterogeneity Hypothesis) for both families of simulations. So, is not surprising that both groups gave similar results.

4. They argued that this approach was 'empirical', free of theoretical assumptions. But in testing between hypotheses, what we are looking for is precisely the differences among theoretical brood-size distributions predicted under the two hypotheses.

5. Summarizing, with the same mean fecundity at high densities, both hypotheses must have different brood-size distributions. So the use of a single left-skewed distribution, typical of a real saturated population (most likely under Habitat Heterogeneity Hypothesis) in attempts to distinguish between the two hypotheses by re-sampling several times on the same left-skewed distribution, as done by Beja & Palma, is clearly inappropriate.

Key-words: brood size distribution, density-dependent fecundity, habitat heterogeneity, individual adjustment, object-orientated simulation.

Introduction

The nature and extent of population regulation by density-dependent processes remains of central concern in population ecology (Ferrer & Donázar 1996; Rodenhouse, Sherry & Holmes 1997; Newton 1998; Penteriani, Balbontin & Ferrer 2003; Sergio & Newton 2003). Identification of proximate mechanisms by which density can affect demographic parameters, as well as the way they operate, is therefore of fundamental interest.

Density-dependent effects in bird population regulation have been well described, especially in fecundity (Newton 1991, 1998; Ferrer & Donázar 1996; Rodenhouse *et al*. 1997). Two major hypotheses have been proposed, in which the observed density-dependent patterns in fecundity could arise either by (1) a higher proportion of individuals occupying poor quality areas at high than at low population densities (Andrewartha & Birch 1954; Pulliam & Danielson 1991; Dhondt, Kempenaers & Adriaensen 1992; Ferrer & Donázar 1996; Krüger & Lindström 2001), or by (2) individuals adjusting their behaviour as a response to changing densities within the same area (Lack 1954; Both 1998). The first mechanism is called the habitat heterogeneity hypothesis (HHH) or site dependence hypothesis (Ferrer & Donázar 1996; Rodenhouse *et al.* 1997), and the second the individual adjustment hypothesis (IAH) or interference competition hypothesis.

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Distinguishing between these two potential regulatory mechanisms is important not only to the theoretical population biologist, but also to the conservation biologist working on endangered species, because it informs management needs (Ferrer & Donázar 1996; Sergio & Newton 2003; Carrete *et al*. 2006; Ferrer, Newton & Casado 2006). Under HHH, populations close to saturation level are perceived as source-sink systems, with pairs in the best parts of the habitat (source areas) producing more young than necessary to replace themselves, and pairs in other parts (sink areas) producing insufficient young, so that their numbers are maintained only by overproduction in source areas (Ferrer & Donazar 1996). Consequently, partial habitat destruction could affect population viability in different ways, depending on which parts of the habitat were affected (Newton 1991, 1998; Ferrer & Donázar 1996). Under IAH, the population is perceived as living in homogeneous habitat, destruction of any part of which should have the same effect on mean reproductive rate as destruction of any other part. For these conservation reasons, several attempts have been made at distinguishing between these two main mechanisms that could produce density dependence in fecundity (see Ferrer & Donazar 1996; Sergio & Newton 2003; Ferrer *et al*. 2006). The methods depend critically on changes in the distribution of brood sizes (including zeros) at different population densities.

Two hypotheses, two distributions

In their paper, Beja & Palma (2007) attempt to provide a critical analysis of the effectiveness and limitations of a previously published method to discriminate between HHH and IAH. To this end, they use real data from a Bonelli's eagle *Hieraaetus fasciatus* population to parameterize a simulation model, which is used to test the skewness and CV trajectories of brood-size distributions according population size. They conclude that, under both hypotheses (HHH and IAH), significant and strong correlations between mean and CV or skewness are expected under a biologically plausible assumption about brood size distribution, and that the two hypotheses cannot therefore be distinguished.

A major concern we have with their paper centres on this biologically plausible brood-size distribution. They used the same quasi-Poisson distribution of brood sizes for both families of simulations (based on HHH and IAH, respectively), because this was the 'real' brood-size distribution in the natural population of eagles. But this distribution could itself result from a density-dependent process, most likely based on HHH (as far as they are able in their study to distinguish between good and bad territories). In any case, they used the same brood size distribution in both groups of simulations, so is not surprising that both groups gave similar results.

Both density-dependent hypotheses generate the same prediction for the distribution of brood sizes in a population at low density, but differ about the final distribution of brood sizes in populations close to saturation level. The idea of different distributions under the two hypotheses was implicit in their formulation. Under IAH, depression in fecundity arises from some factor that acts more or less uniformly across the population, such as an increasingly hostile social environment resulting from increasing agonistic encounters and interference that has a similar impact on all individuals. As density rises, practically all individuals could show reduced fecundity, and variance in brood sizes among individuals would not alter (Lack 1966; Fretwell & Lucas 1970; Dhondt & Schillemans 1983; Ferrer & Donazar 1996). In contrast, under HHH, the depression of mean fecundity results from habitat heterogeneity, and as density rises, an increasing proportion of individuals are forced to occupy poorer habitat, where individual reproductive rates are lower. During a period of population increase therefore mean population brood-size decreases while variance in brood size increases (Andrewartha & Birch 1954; Brown 1969; Fretwell & Lucas 1970; Dhondt *et al*. 1992; Ferrer & Donazar 1996). It is true that nothing about the real form of the distribution was said, but it is clear that, with the same mean fecundity, the two hypotheses must have different brood-size distributions. As density rises, the HHH predicts an increasingly left-skewed distribution of brood sizes, with some territories producing consistently large broods, against an increasing number producing smaller broods. Conversely, the IAH predicts a closer-to-normal distribution of brood sizes at all densities, centred on a decreasing mean value as density rises. It is this distribution of brood sizes, or its change during population growth, which is crucial to testing between the two hypotheses.

The bootstrapping procedure used by Beja & Palma (2007) is a general technique for estimating sampling distributions by treating the observed data as if it were the entire (and unique) statistical population under study. On each replication, a random sample of size *N* is selected, with replacement, from the available data. Under HHH, Beja & Palma divided their territories, on the basis of brood sizes, into good and bad, sampling from good and poor territories separately and after pooling them. Under IAH, they sampled only from the total data base (of both good and poor territories) and presented the results altogether. (Note that some of the outliers are the same in the two 'different' families of simulations.) They argued that this approach was 'empirical', free of theoretical assumptions. But in testing between hypotheses, what we are looking for is precisely the differences among theoretical brood-size distributions predicted under the two hypotheses.

It is the left-skewed brood-size distribution universal among long-lived birds?

Beja & Palma (2007) claimed that long-lived species with low fecundity often show left-skewed brood-size distributions (close-to-Poisson) regardless of situation. They concluded that the use of a close-to-normal distribution in Ferrer *et al*. (2006) was an unrealistic approach, likely to generate spurious correlations. Nevertheless, a quasi-normal distribution of brood sizes is the most common situation in raptor populations at low densities (see Ferrer & Donazar 1996). Interestingly, using their own data on brood sizes in good territories (the

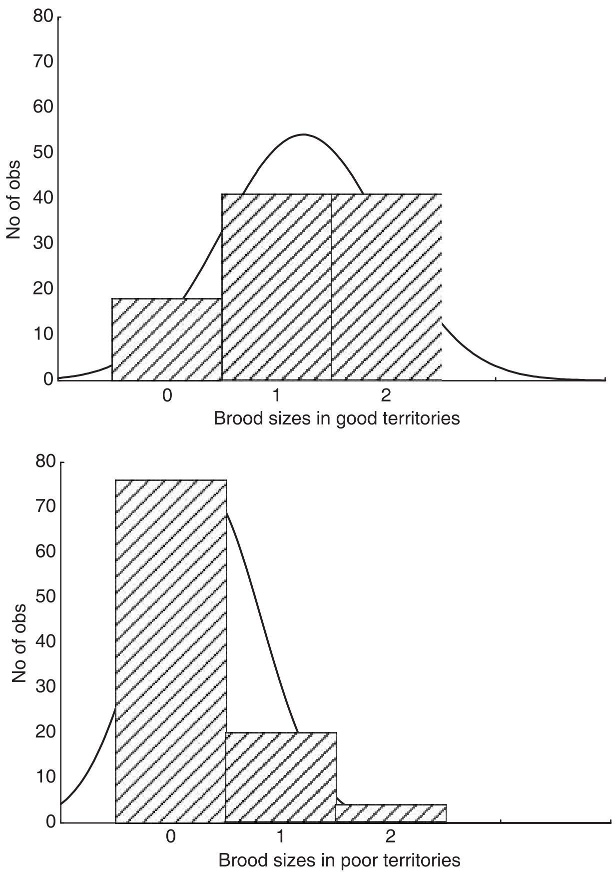

Fig. 1. (a) Using data from Beja & Palma (2007), at low density, brood sizes of Bonelli's Eagles showed a non-left-skewed distribution. (b) Poisson (left-skewed) distribution of brood sizes in poor territories of Bonelli's Eagles (those occupied only in a high-density situation, data from Beja & Palma 2007).

only territories occupied at low density) in their Bonelli's eagle's population, the distribution of brood sizes was close-to-normal, showing no left-skew (Fig. 1a). In contrast, their data from poor territories (those occupied only in a high-density situation) showed a strong left-skewed distribution (Fig. 1b). This is as expected under HHH.

Nevertheless the number of brood-size categories will clearly influence the power of the test, and the likelihood of obtaining a significant test result. The Spanish Imperial Eagles *Aquila adalberti* discussed in our original paper had four brood size categories (0–3), while their Bonelli's eagles had three (0–2). In species that lay only one egg (brood sizes 0 or 1), it is extremely unlikely that the two hypotheses could be distinguished using this kind of approach. But as the number of brood size categories increases, it should become increasingly easy to detect differences between the two expected distributions.

Simulation problems

Beja & Palma stated that the use of the normal distribution is unwarranted because it causes simulation problems, such as predicted values below zero. It is true that using a normal distribution, when mean fecundity values decrease, some of the randomly selected values would be less than zero, but this problem can be corrected easily during the simulation, first by raising negative values to zero, which gives a mean value slightly higher than the stipulated mean. This higher mean must then be reduced accordingly for the next simulation. These correction procedures were employed in Ferrer *et al.* (2006).

Owing to scant procedural details, we find it difficult to follow the logic of the simulation in Beja & Palma (2007), but nevertheless it is easy to see that simulations of increasing populations were done starting with a mean fecundity of 1·23 (corresponding to mean value for high-quality sites) and ending with 0·28 (corresponding with the mean value for low-quality sites, see table 1 of Beja & Palma 2007). By this procedure, they effectively forced the whole final population into in low-quality sites (or greatly affected by interference) with a mean fecundity far below the observed, which seems to be about 0·75 (see Fig. 1 in Beja & Palma 2007). They thereby constrained the results of the simulation into an unrealistic and extremely left-skewed distribution. With this extremely low mean value of 0·28, the population would probably become extinct without continuing immigration.

Spurious correlations

Beja & Palma stated that the regression relationship between mean fecundity and its coefficient of variation should not be used in further studies owing to potential spurious correlation in the general form of *X* vs. *Y*/*X*, in which *X* and *Y* are nonindependent variables. We agree that caution should be exercised, as stressed in our previous paper, but disagree that only spurious correlations are expected (a point also made by Brett (2004) cited by the authors in support of their view). According to Chayes (1949), the expected spurious correlation of the form *X* vs. *Y*/*X* is:

$$r = -\mathrm{CV}_x/(\mathrm{CV}_y^2 + \mathrm{CV}_x^2)^{1/2}$$

Using data from our previous paper, the expected coefficient of determination due to spurious correlation was $r^2 = 0{\cdot}54$ for an increasing population under IAH and $r^2 = 0{\cdot}52$ for an increasing population under HHH. The values obtained in the previous analyses were $r^2 = 0{\cdot}511$ for increasing population under IAH and $r^2 = 0{\cdot}92$ for increasing populations under HHH. This implies that the relationship found between mean fecundity and its CV under IAH could have been solely the result of a spurious correlation, as stated by Ferrer *et al.* (2006). But the relationship found in an increasing population under HHH between mean fecundity and its CV is clearly stronger than expected solely due to spurious correlation. To adequately analyse this problem when using the relationship between mean fecundity and CV to look for density dependence, we have to use the above approach or conduct simulations using, for example, the Monte Carlo procedure to generate the null distribution against which we can test the significance of the correlation coefficients. These problems complicate the use of CV and mean fecundity as a clear test to discriminate between the two main hypotheses, as stated in our previous paper. On the other hand, this kind of problem does not arise in the relationship between mean brood size and skewness. For this reason among others, we suggest the use of this test (Ferrer *et al*. 2006).

Beja & Palma stated that, by and large, caution should be exercised when interpreting results of previous studies relying on the mean fecundity–CV relationship to draw inferences about population processes (they cited Ferrer & Donazar 1996; Blanco *et al*. 1998; Krüger & Lindström 2001; Penteriani *et al*. 2003; Sergio & Newton 2003; Carrete *et al*. 2006). However, as is clearly evident in the papers they cited, all the authors used several different and complementary criteria, including the CV test, in drawing conclusions about which mechanism was the most relevant in their study populations. So the concerns expressed by Beja & Palma do not seem well supported in practice.

Beja & Palma further stated that our previous suggestion of the use of the skewness test as the simpler way to differentiate between density-dependent fecundity hypotheses was largely inadequate. We believe that they are too dismissive of the test we propose. We did not claim that this test was the only and definitive way to assess the kind of regulation operating. We said that, if a significant test result is obtained, this provides strong support for the overwhelming operation of HHH. If the result is statistically insignificant, this does not wholly exclude the operation of HHH, but indicates that its role is small compared with other mechanisms of density dependence. As stated in Ferrer *et al*. (2006), additional criteria are recommended, namely: (1) high-quality yield similar brood sizes at high or low population densities under HHH; (2) high-quality sites are the first and most frequently occupied sites; (3) high-quality sites are less variable in productivity among years than low-quality sites; or (4) low-quality sites may be more frequently occupied by nonadult individuals in species with deferred sexual maturity. Use of all these criteria requires a good data base. When only long-term data on brood size are available, the use of the skewness test seems ideal to check for the operation of one of these regulatory mechanisms.

Habitat and individual quality

Beja & Palma also stated that Carrete *et al*. (2006) reported immature birds breeding more frequently in certain territories than expected by chance, and concluded that differences in fecundity among territories could arise simply from variability in occupant age rather than in territory quality. While the age of an eagle it is without doubt an eagle characteristic, differences in the probability of occupancy of territories by immature birds seems to be a characteristic of the territories themselves, being a component of territory quality. Hence, the differences in brood sizes they detect are in fact partly a consequence of the differences in territory quality, specifically in the turn-over rates. This is true irrespective of the possible cause generating these differences (mortality, emigration rate, etc.). As stated by Ferrer & Bisson (2003), heterogeneity in individual performance within populations need require only two assumptions: (1) breeding outputs differ among territories, and/or (2) occupant turnover rates by either mortality or emigration differ among territories.

Conclusions

In conclusion, the HHH predicts an increasingly left-skewed distribution of brood sizes as density rises, with only some territories producing consistently large broods, and an increasing number producing few or no chicks. Conversely, the IAH predicts a more close-to-normal distribution of brood sizes at all densities with only minor differences among territories. Consequently, with the same mean fecundity at high densities, both hypotheses must have different brood-size distributions (Fig. 2). So the use of a single left-skewed distribution, typical of a real saturated population (most likely under HHH) in attempts to distinguish between the two hypotheses by re-sampling several times on the same left-skewed distribution, as done by Beja & Palma (2007), is clearly inappropriate.

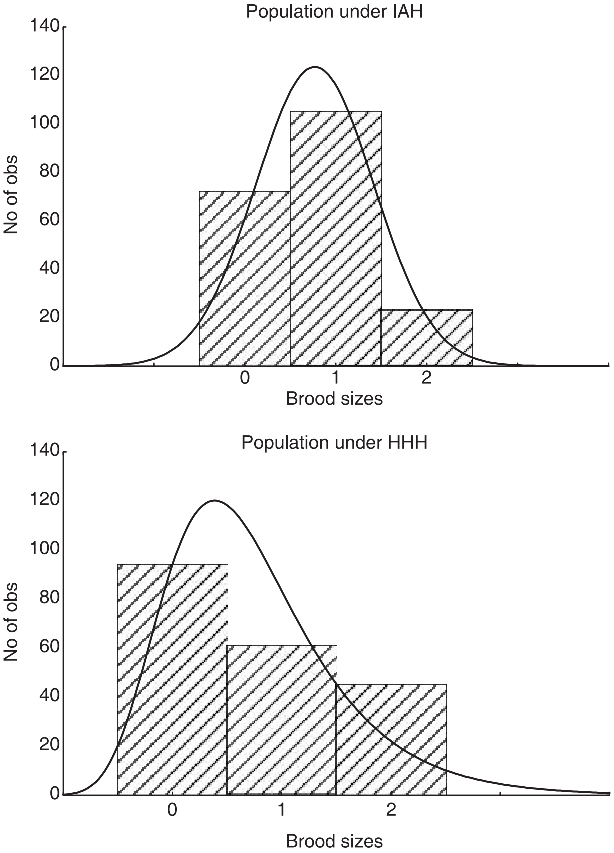

Fig. 2. (a) Non-left-skewed brood sizes distribution of Bonelli's Eagles in a saturated population with a mean fecundity of 0·75 (i.e. under IAH). (b) Brood sizes distribution in a saturated population under HHH with a mean fecundity of 0·75 showing a quasi-Poisson distribution (using data from Beja & Palma 2007).

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