How to test different density-dependent fecundity hypotheses in an increasing or stable population

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Summary

1. We report on a simulation study of increasing and stable populations working under two different hypotheses of density dependence of fecundity: the habitat heterogeneity hypothesis (HHH) and the individual adjustment hypothesis (IAH). Our aim is to find critical differences between the two regulatory hypotheses in natural populations.

2. Populations under HHH show a strong negative relationship between fecundity and the coefficient of variation of fecundity. We also found a strong negative relationship between fecundity and skewness, demonstrating that, as fecundity decreases, the form of the distribution of brood sizes changes, being more left-skewed due to more territories failing to produce any offspring.

3. This strong relationship was found only in the simulations of populations under HHH; whether increasing or stable, and under different ratios of good : poor territories and different population sizes. In contrast, no relationship between mean fecundity and skewness was found among simulations under IAH.

4. Populations under IAH also showed a significant relationship between mean fecundity and the coefficient of variation of fecundity, but with a lower slope than in populations under HHH.

5. In conclusion, skewness was found to be an adequate critical test that showed significant and strong relationships with mean fecundity only in populations under HHH, whether increasing or stable. This test is useful for species with a discrete distribution of offspring with a small number of integer categories, including most of the bird and mammal species.

Key-words: *Aquila adalberti*, density-dependent fecundity, habitat heterogeneity, individual adjustment, population dynamics.

Introduction

The nature and extent of population regulation by density-dependent processes remains a central question in population ecology (Newton 1994; Ferrer & Donázar 1996; Rodenhouse, Sherry & Holmes 1997; Newton 1998; Penteriani, Balbontin & Ferrer 2003). Identification of proximate mechanisms by which density can affect demographic parameters is of fundamental importance in ecology. Density-dependent effects in population

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regulation have been well described, especially in fecundity (Newton 1991, 1998; Ferrer & Donázar 1996). However, operating mechanisms are unclear, although two major hypotheses have been proposed (Fretwell & Lucas 1970). The observed density-dependent patterns in mean fecundity could arise either by a higher proportion of individuals occupying poor quality habitats in a heterogeneous environment at high population densities (Andrewartha & Birch 1954; Pulliam & Danielson 1991; Dhondt, Kempenaers & Adriaensen 1992; Ferrer & Donázar 1996; Krüger & Lindström 2001), or by individuals adjusting their behaviour as a response to changing densities within the same habitat, with density affecting all territories and individuals equally (Lack 1954; Both 1998; Fernandez, Azkona & Donázar 1998). The first mechanism is called the

habitat heterogeneity hypothesis (HHH) (Dhondt *et al.* 1992; Ferrer & Donázar 1996). According to these authors, as density rises, an increasing proportion of individuals is relegated to lower quality habitats, as a result of which mean population fecundity declines (Andrewartha & Birch 1954; Brown 1969). The second mechanism is named the individual adjustment hypothesis (IAH) or interference competition hypothesis. According to some authors (Lack 1966; Fretwell & Lucas 1970; Dhondt & Schillemans 1983; but see Kempenaers & Dhondt 1992), density-dependent depression of fecundity can arise from an increased frequency of aggression and interference among territorial pairs, resulting in a hostile social environment that leads to a relatively uniform decrease in bird performance. On this hypothesis, as densities increase, all individuals should show reduced fecundity.

As stated by Ferrer & Donázar (1996), these two hypotheses generate the same predictions about mean fecundity in an increasing population: as density rises, mean fecundity declines. Predictions for the expression of fecundity variance, however, are different. For the IAH, no relationship is expected but for the HHH, fecundity variance must increase with density, because at high densities more poor sites (giving lower fecundity) are occupied. In consequence, Ferrer & Donázar (1996) suggested that a critical test between the two regulatory mechanisms in an increasing population would be a strong negative relationship between mean fecundity and its coefficient of variation. This test was subsequently used by several authors (Krüger & Lindström 2001; Penteriani, Gallardo & Roche 2002; Sergio & Newton 2003). Nevertheless, the possibility of spurious correlations between the mean and coefficient of variation in a discrete distribution, with a small number of categories and limited by boundaries, such as brood-size distribution in birds or litter size in mammals, leads us to search for complementary criteria.

Here, we report on an individual-based simulation study of increasing and stable model populations, one pair working as predicted by HHH and the other as predicted by IAH. Our aim is to analyse changes in the parameters of the distribution of both types of populations in an attempt to find critical differences that allow us to discriminate clearly between the two regulatory hypotheses in natural populations, whether these populations are increasing or stable (or declining). Additionally, we use data from a population of the Spanish Imperial Eagle *Aquila adalberti* Brehm 1861 in Doñana National Park (south-west Spain) as a case study.

Materials and methods

COMPUTER SIMULATION AND MODEL ASSUMPTIONS

Individual-based models envisage a population as an assemblage of individuals. They have been applied to a wide variety of ecological problems (Lomnicki 1978;

Huston, DeAngelis & Post 1988; DeAngelis & Gross 1992; Uchmanski & Grimm 1996; Fahse, Dean & Wissel 1998; Wilson 1998; Grimm 1999; Ferrer, Otalora & García-Ruiz 2004), and have a number of advantages over other, more traditional types of modelling techniques. In our case, we developed a stochastic 'territory-based' simulation, using turbo Pascal to model the dynamics of the population. Breeding outputs of up to 30 territories were simulated simultaneously. In this way we created a 'simulated breeding population' from which 'simulated field data' were obtained.

Simulation models were adjusted as appropriate to breeding parameters of the *A. adalberti*, using data of a well-known population in Doñana National Park, south-west Spain (Ferrer & Calderón 1990; Ferrer & Donázar 1996; Ferrer 2001; Ferrer *et al.* 2004). The *A. adalberti* is a large (2500–3500 g), sedentary and territorial bird of prey, with a low reproductive rate and a relatively high age of maturity (adult plumage at age 4–5 years). Territories, with a mean size of 1200 ha, are exclusive and vigorously defended throughout the year. Models were used to generate the expected distribution of brood sizes in theoretical populations of eagles that can only have four integer values of brood size: none, one, two and three nestlings. This represents a common and realistic scenario for most territorial raptors, owls and other species of birds (Newton 1979; Del Hoyo, Elliot & Sargatal 1994) as well as for most of the mammals. We used a time step of 1 year. Territories were created and decisions about their production each year were made through the use of random number generators. For each cycle (equivalent to 1 year), we computed the number of active territories and number of offspring produced in each. We also computed the mean and the variance of fecundity by years and by territories. We made 200 replicates of the same population, and the simulation closest to the mean of all the 200 replicates of each case was selected. This allowed us to work with a brood-size distribution having a discrete, small number of categories, limited by boundaries, as in many large birds.

SIMULATIONS UNDER HABITAT HETEROGENEITY HYPOTHESIS

Two different situations were simulated, involving increasing and stable populations. The increasing populations were allowed to increase from a starting number of 10 pairs until they reached the ceiling number of 30 pairs, and simulations were run for 30 breeding seasons (equal to years). During this period of population increase, we included a decrease in fecundity according to a density-dependent fecundity function that reduced fecundity linearly from starting values of 1·59 to final values of 0·7 young per pair (44% of the initial mean fecundity, Ferrer & Donázar 1996). As we assumed that density-dependent fecundity arose by the HHH, we maintained the same fecundity values from the beginning (low density situation) until the end

(saturated situation) in the first-occupied territories. In consequence, the decrease in mean fecundity was due only to the occupation of new territories, where birds had lower fecundity. Two different ratios between good : poor territories were used: 10 high quality territories from a total of 30, and 10 poor from a total of 30. To account for stochasticity in fecundity values, we selected for each territory each year one value at random from a normal distribution with mean fecundity according to density and territory quality (high quality territories: 1·59 nestlings; low quality: 0·47 nestlings, in the real population fecundity was normally distributed, see Ferrer & Donázar 1996), and variance according to observed variance in the natural population, that is 0·901 (Ferrer & Donázar 1996; Ferrer *et al*. 2004). The integer value closest to the random number was selected as brood size for the territory. During population increase, low quality territories were only occupied when no high quality one was unoccupied.

We also simulated stable populations that stayed at the ceiling level of 30 pairs over 30 years with a mean fecundity value for the whole population of 0·7 young per pair per year. Again, two different ratios of good : poor territories were used (10 : 20 and 20 : 10). For each territory each year, one value at random from a normal distribution was selected. In the high quality territories, mean fecundity was 1·59 and in the low quality territories 0·47, with variance again set at 0·901. Simulations during a short time, 10 years, were also conducted to analyse the effect of sample size (numbers of years), as well as small populations with only 15 breeding pairs (five good and 10 poor territories).

SIMULATION UNDER INDIVIDUAL ADJUSTMENT HYPOTHESIS

Here we again simulated two different situations. The increasing population was allowed to increase from 10 to 30 territories during 30 years, using the same density-dependent fecundity function that above. As we assumed that density-dependent regulation of fecundity was by IAH, we used the same mean fecundity for all the territories (mean according density and variance of 0·901). So as density increased, fecundity decreased with the same probability in all the territories. To account for stochasticity in fecundity values, we selected for each territory each year one value at random from a normal distribution with mean fecundity according density (low density 1·59; high density 0·7, the same value for all the territories), and variance according to observed variance in the natural population (that is 0·901, see above). The integer value closest to the random number was selected as the brood size for the territory. During the period of population increase, new territories were occupied at random.

We also simulated 30 years of a stable population that stayed at the ceiling level of 30 pairs, with a mean fecundity value for the whole population of 0·7. Again, we selected for each territory each year one value at

random from a normal distribution, but in this occasion, mean fecundity was 0·7 (mean value for eagle populations under saturation) for all the territories, and variance was again 0·901. Ten-year simulations with 30 and 15 pairs were also conducted to analyse the possible effect of sample size.

REAL POPULATION DATA

The *A. adalberti* is the most endangered bird of prey in Europe and one of the rarest raptors in the world (Collar & Andrew 1988). Its total population is estimated to be about 150 pairs (Ferrer 2001). In Doñana National Park, its numbers increased from six to 15–16 breeding pairs, and then remained stable from 1976 until 1992 (long-term monitoring data (1959–91) from the Doñana archives). From this pattern, it may be inferred that the population was close to the environmental carrying capacity during the last years. Coincident with the population increase, mean fecundity followed an inverse trend, decreasing and then stabilizing with population size. The entire National Park area was surveyed at the beginning of each breeding season (January–February, during the courtship and nest site selection period; Ferrer 2001) to determine if pairs were present on territories. The sedentary behaviour of birds and their tendency to call repeatedly greatly facilitated detection of territorial pairs. We believe that all breeding and nonbreeding pairs were detected every year.

STATISTICAL ANALYSES

Statistical analyses were conducted using STATISTICA package. All the variables were normally distributed. We tested for trends with linear analysis using the *F*-ratio statistic to find whether the slope of the data was significantly different from 0. Variances of the linear models were tested for homogeneity using Cochran's C statistic. Mixed ANOVAs with random factors were employed. Statistical significance was set at $P < 0·05$.

Results

POPULATIONS UNDER HABITAT HETEROGENEITY HYPOTHESIS

Coefficient of variation of fecundity in an increasing population with a good : poor territory ratio of 10 : 20, showed a significant increase from 45% to 130% as the population increased from 10 to 30 pairs (Fig. 1). Mean fecundity, coefficient of variation of fecundity, skewness and kurtosis showed highly significant relationships with population density (four-way ANOVA; fecundity, $F = 139·31$, d.f. = 4, 26, $P < 0·001$; CV, $F = 54·43$, d.f. = 4, 26, $P < 0·001$; skewness, $F = 43·40$, d.f. = 4, 26 $P < 0·001$; kurtosis, $F = 3·18$, d.f. = 4, 26, $P = 0·03$). As population density increased, coefficient of variation, skewness and kurtosis increased, while fecundity decreased. Mean fecundity was inversely
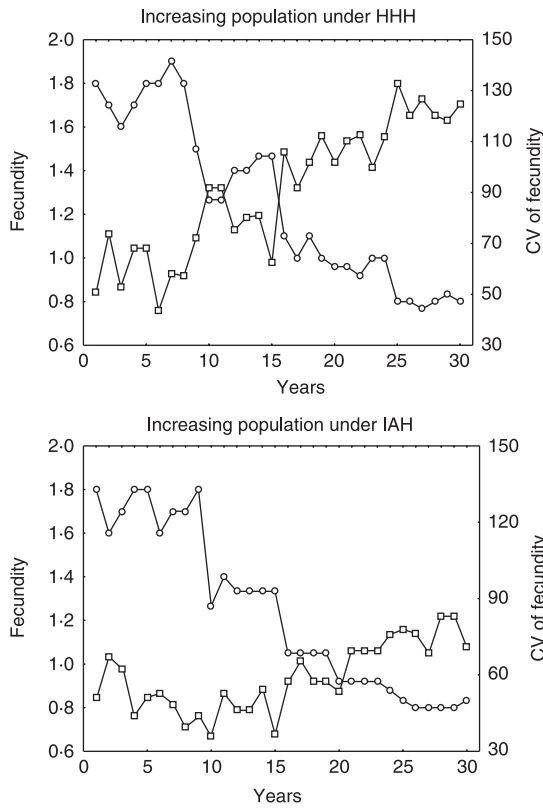
Fig. 1. Trend of mean (○) and coefficient of variation (□) of fecundity in increasing simulated populations according to habitat heterogeneity and individual adjustment hypotheses.
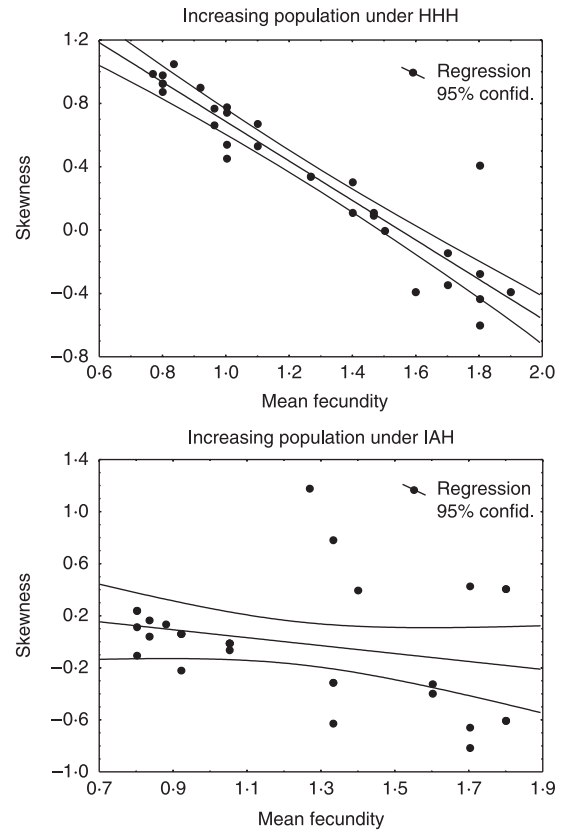

Fig. 2. Linear regressions between skewness and mean fecundity in increasing simulated populations according to habitat heterogeneity and individual adjustment hypotheses.

related to skewness of fecundity (Fig. 2). In addition, coefficient of variation showed significant variation according to mean fecundity (Table 1).

Using a ratio of 20 good to 10 poor territories, again mean fecundity, coefficient of variation, skewness and kurtosis showed highly significant relationships with population density (four-way ANOVA; fecundity, $F =$ 14·16, d.f. = 4, 26, $P < 0·001$; CV, $F = 7·80$, d.f. = 4, 26, $P < 0·001$; skewness, $F = 4·72$, d.f. = 4, 26 $P < 0·001$; kurtosis, $F = 0·65$, d.f. = 4, 26, $P = 0·652$). As the model population grew, coefficient of variation of fecundity and skewness increased, and fecundity decreased. Coefficient of variation of fecundity was inversely related to mean fecundity, as was skewness (Table 1).

Table 1. Results of linear regressions with mean fecundity as the independent variable and coefficient of variation (CV), skewness and kurtosis as dependent variables. Simulations were made under different hypotheses, ratios of good : poor quality territories, population trends (increasing or stable populations) and during different number of years (see text)

Hypothesis	Pairs	Fecundity	Years	Good : poor	CV			Skewness			Kurtosis		
					r	d.f.	P	r	d.f.	P	r	d.f.	P
HHH-increasing	10–30	1·6–0·7	30	10 : 20	−0·954	28	**	−0·935	28	**	−0·412	28	*
HHH-increasing	10–30	1·6–0·7	30	20 : 10	−0·682	28	**	−0·770	28	**	0·124	28	NS
IAH-increasing	10–30	1·6–0·7	30	–	0·715	28	**	−0·258	28	NS	−0·193	28	NS
HHH-stable	30	0·7	30	10 : 20	−0·715	28	**	−0·926	28	**	−0·383	28	*
HHH-stable	30	0·7	10	10 : 20	−0·939	8	**	−0·877	8	**	−0·635	8	*
HHH-stable	30	0·7	30	20 : 10	−0·898	28	**	−0·786	28	**	0·466	28	*
HHH-stable	30	0·7	10	20 : 10	−0·945	8	**	−0·735	8	**	0·551	8	*
HHH-stable	15	0·7	30	5 : 10	−0·545	28	**	−0·652	28	**	−0·110	28	NS
HHH-stable	15	0·7	10	5 : 10	−0·492	8	NS	−0·879	8	**	−0·162	8	NS
IAH-stable	30	0·7	30	–	0·474	28	*	0·301	28	NS	0·579	28	**
IAH-stable	30	0·7	10	–	0·672	8	*	0·124	8	NS	0·445	8	NS
IAH-stable	15	0·7	30	–	0·674	28	**	−0·183	28	NS	0·325	28	NS
IAH-stable	15	0·7	10	–	0·317	8	NS	0·103	8	NS	0·621	8	*

**$P < 0·001$; *$P < 0·5$; NS, not significant.

Simulations of stable populations under HHH with 10 good territories of 30 over a period of 30 years showed that the coefficient of variation was inversely related to mean fecundity, as was skewness (Table 1). Reducing the simulation time to 10 years to analyse the possible effect of length of study, we obtained the same results (Table 1) as well as on a good : poor territory ratio of 20 : 10 (Table 1). Ten-year simulations with a 20 good : 10 poor territory ratio showed that the coefficient of variation and skewness were significantly related with mean fecundity (Table 1).

Simulations conducted with populations of only 15 pairs (five good and 10 poor territories) over 30 years showed significant relationships between mean fecundity and coefficient of variation and skewness (Table 1). Reducing the simulation period to 10 years again revealed a significant relationship between mean fecundity and skewness, but not with coefficient of variation (Table 1).

POPULATIONS UNDER INDIVIDUAL ADJUSTMENT HYPOTHESIS

The coefficient of variation of fecundity in an increasing population under IAH increased from 45% to 80% as the population increased from 10 to 30 pairs (Fig. 1). Only mean fecundity and its coefficient of variation showed highly significant relationships with population size, but not skewness or kurtosis (four-way ANOVA; fecundity, $F = 365 \cdot 56$, d.f. = 4, 26, $P < 0 \cdot 001$; CV, $F = 17 \cdot 26$, d.f. = 4, 26, $P < 0 \cdot 001$; skewness, $F = 1 \cdot 03$, d.f. = 4, 26 $P = 0 \cdot 409$; kurtosis, $F = 0 \cdot 717$, d.f. = 4, 26, $P = 0 \cdot 588$). The coefficient of variation was inversely related to mean fecundity (Table 1). In contrast, skewness was not related to mean fecundity (Fig. 2).

Simulations of stable populations under IAH over 30 years showed that the coefficient of variation was inversely related to mean fecundity, while skewness showed no significant relationship (Table 1). Ten-year simulations showed a significant negative relationship between mean fecundity and coefficient of variation, but not with skewness (Table 1).

Simulations with a population of only 15 pairs over 30 years also showed a significant negative relationship between mean fecundity and coefficient of variation, but not with skewness (Table 1). Ten-year simulations with 15 pairs showed that mean fecundity was not related to coefficient of variation, or skewness (Table 1).

REAL POPULATION

The proportion of high vs. low quality territories in the real population was 6 : 10 (Ferrer & Donázar 1996). Mean fecundity was negatively related to coefficient of variation of fecundity ($r = -0 \cdot 890$, d.f. = 23, $P < 0 \cdot 001$; Ferrer & Donázar 1996), and to skewness ($r = -0 \cdot 860$, d.f. = 23, $P < 0 \cdot 001$). In addition, kurtosis showed significant variation according to mean fecundity ($r = -0 \cdot 656$, d.f. = 23, $P < 0 \cdot 001$).

Discussion

Simulation models enable us to analyse differences in the distribution of parameters according to the mechanisms used to generate density-dependent depression of fecundity. Increasing populations under HHH showed a strong negative relationship between fecundity and coefficient of variation of fecundity: as population size increased, mean fecundity decreased and coefficient of variation increased. We found a strong negative relationship between fecundity and skewness, demonstrating that as fecundity decreased, the form of the distribution of brood sizes changed, being more left-skewed. This strong relationship was found in the simulations of populations under HHH; whether increasing or stable, and under different ratios of good : poor territories and different population sizes. Also a significant relationship between mean fecundity and coefficient of variation was found in stable populations under HHH.

On the other hand, significant negative relationships between fecundity and coefficient of variation of fecundity in increasing and stable populations under IAH were found. As fecundity decreased, coefficient of variation increased significantly, but with a lower slope than in populations under HHH. In contrast, no relationship between mean fecundity and skewness was found among simulations under IAH, whether in increasing or stable populations, or in populations of different sizes.

Using data from a real population of eagles known to be under density-dependent regulation of fecundity through habitat heterogeneity (Ferrer & Donázar 1996), a strong negative relationship between mean fecundity and skewness was found.

In consequence, the suggestion of Ferrer & Donázar (1996) that a critical test between the two regulatory mechanisms in an increasing population would be a strong negative relationship between mean fecundity and its coefficient of variation under HHH but not under IAH, must be taken with caution. In fact, this expected relationship is true and strong in populations under HHH, but could also emerge as statistically significant in populations under IAH. The reason is that, in a discrete integer distribution, with a low number of brood-size categories and limited by fixed boundaries, spurious correlations between the mean value and the coefficient of variation can be found. As brood size and litter size distributions are limited by fixed boundaries (for example, it is impossible to have a negative fecundity), as mean fecundity decreases, variance of fecundity would increase. So the differences in the relationship between mean fecundity and coefficient of variation among both hypotheses is only a matter of degree.

On the other hand, skewness was found to be an adequate critical test that showed significant and strong relationships with mean fecundity only in populations under HHH, whether increasing or stable. Skewness is at best as an indicator of changes in the form of distributions fitting well with the original idea of different

parts of the population responding in different ways to density changes, whether long-term or year-to-year. A important point is that results seem to show that the skewness test is a very robust one, even when a short time series was used. That would mean that this test could be used even with relatively few data.

Of course, additional criteria could distinguish between the two hypotheses, for example: (1) high quality sites have the same fecundity at high or low population densities (Newton & Marquiss 1976; Newton 1991; Ferrer & Donázar 1996; Rodenhouse *et al.* 1997); (2) high quality sites must be the first and most frequently occupied sites (Ferrer & Donázar 1996; Sergio & Newton 2003); or (3) high quality sites must be less variable among years than low quality sites (Ferrer & Donázar 1996). Another complementary criterion is that low quality sites may be more frequently occupied by nonadult individuals in species with deferred sexual maturity (Ferrer & Bisson 2003; Ferrer & Penteriani 2003). However, use of all these criteria requires a good data-base with all occupied sites, territories and occupants monitored year after year. Such studies are not so common, and more often we have access only to a long series of fecundity data with no clear geographical reference points. For these types of data, the present test of coefficient of variation and skewness seems ideal to find the mechanism of density dependence over the prevailing density range.

With the skewness test, we are able to determine whether the response of a population to long-term changes in density or to interannual fluctuations in density is heterogeneous or not. Territory quality is not necessarily the only source of heterogeneity; however, for breeding success is a function of both territory quality and individual quality. If the best territories were occupied by the best performing animals, rather than by a random selection of animals, this would add to the level of heterogeneity resulting from territory quality alone (Newton 1991; Ferrer & Donázar 1996; Rodenhouse *et al.* 1997). Whatever its cause, the existence of consistent heterogeneity is always important from a theoretical point of view, as well as for informing conservation programmes.

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