43 Burke, T. *et al.* (1989) Parental care and mating behaviour of polyandrous dunnocks *Prunella modularis* related to paternity by DNA fingerprinting, *Nature* 338, 249–251

44 Møller, A.P. and Birkhead, T.R. (1993) Cuckoldry and sociality: a comparative study, *Am. Nat.* 142, 118–140

45 Lifjeld, J.T., Dunn, P.O. and Westneat, D.F. (1994) Sexual selection by sperm competition in birds: male–male competition or female choice? *J. Avian Biol.* 25, 244–250

46 Clutton-Brock, T.H. and Parker, G.A. (1995) Punishment in animal societies, *Nature* 373, 209–216

47 Møller, A.P. (1992) Frequency of female copulations with multiple males and sexual selection, *Am. Nat.* 139, 1089–1101

48 Alatalo, R.V. *et al.* (1996) Paternity, copulation disturbance and female choice in lekking black grouse, *Anim. Behav.* 52, 861–873

49 Lank, D.B. *et al.* (1995) Genetic polymorphism for alternative mating behaviour in lekking male ruff *Philomachus pugnax*, *Nature* 378, 59–62

Reference added in proof

50 Westneat, D.F. and Sherman, P.W. (1997) Density and extra-pair fertilizations in birds: a comparative analysis, *Behav. Ecol. Sociobiol.* 41, 205–215

Population dynamics of large herbivores: variable recruitment with constant adult survival

Jean-Michel Gaillard, Marco Festa-Bianchet and Nigel Gilles Yoccoz

The factors that explain changes in population size are a central theme in ecology, and long-term studies of population dynamics are of great interest for life history theory, population ecology, wildlife management and conservation biology[1,2]. Studies that can identify which vital rates are more variable (variability patterns) and which ones are more likely to influence overall changes in population size (elasticity patterns) are particularly useful[2]. Historically, large herbivores were sometimes considered unsuitable for the study of population ecology because their long generation time meant that interesting results could not be expected for several years. However, large herbivorous mammals are particularly suited to demographic studies because age classes are readily identifiable. In addition, many species are economically important or are useful indicator species for conservation. Recently, several researchers have published long-term studies of ungulates, mostly based on monitoring of marked individuals and often taking advantage of recent methodological developments of Capture–Mark–Recapture (CMR) modeling that account for differences in the probability of recapturing (or resighting) marked individuals, so that biological hypotheses can be tested reliably[3].

Recent studies suggest that the population dynamics of large herbivores can be strongly affected by a combination of stochastic environmental variation and density dependence[4]. Food resources, habitat quality, weather, disease and parasites, interspecific competition, predation, human activities and population density can account for the demographic variation observed among years within a population or among populations within a species. While several studies have

Recent long-term studies of population ecology of large herbivorous mammals suggest that survival of prime-aged females varies little from year to year and across populations. Juvenile survival, on the other hand, varies considerably from year to year. The pattern of high and stable adult survival and variable juvenile survival is observed in contrasting environments, independently of the main proximal sources of mortality and regardless of whether mortality is stochastic or density-dependent. High yearly variability in juvenile survival may play a predominant role in population dynamics.

Jean-Michel Gaillard, Marco Festa-Bianchet and Nigel Gilles Yoccoz are at the UMR CNRS 5558, Laboratoire de Biométrie, Génétique et Biologie des Populations, Université Lyon 1, 43 Boulevard du 11 novembre 1918, 69622 Villeurbanne Cedex, France (gaillard@biomserv.univ-lyon1.fr).

attempted to identify the most important factor driving changes in population size (e.g. Ref. 2), less effort has been devoted to assessing the roles of different vital rates (such as age-specific survival and reproduction) in affecting population dynamics. Because large herbivores have strongly age-structured populations and markedly iteroparous life histories[5], different vital rates may respond differently to various limiting factors (Box 1). Twenty years ago, Eberhardt[6] proposed that the negative effects of increasing density on population growth would occur in a specific order. Among vital rates, juvenile survival (usually defined as survival over the first year of life) should change first, then the age at first reproduction, followed by the reproductive rates of prime-age adults and lastly by adult survival (Box 1).

Here, we review recent research trends on temporal variation in survival of juveniles and of prime-aged females in response to environmental stochasticity and density-dependence in large herbivores. We do not discuss demographic variation because we excluded accounts of small populations where demographic stochasticity could account for an important part of stochastic variation in vital rates.

Assessing temporal variation in vital rates in wild populations: methods and data

Two fundamental problems in population dynamics have challenged biologists and statisticians[2]: (1) how to measure the contribution of different vital rates to overall variability in population growth rate, and (2) how to quantify the roles of density-dependent and density-independent factors. Reliable estimates of each vital rate and a measure of the precision of these estimates (such as their variance) are key

to solving these problems. Until very recently, reliable estimates of vital rates (especially survival) for wild populations of large herbivores were uncommon, because they require long-term monitoring of marked individuals. Most published survival estimates were based on transversal life tables (for instance 14 of 17 ungulate populations in Purvis and Harvey's analysis[7]). The life-table technique assumes a stationary age distribution and equal probability of sampling for all individuals: if these assumptions are violated, survival estimates are unreliable[1]. These strict assumptions are unlikely to be met in any population of wild mammals[8,9]. Even if the assumptions were met, life-table methods do not generally provide any measure of variability in survival rates.

Fortunately, recent years have seen a rapid increase in use of CMR and radiotelemetry methods for estimating survival rates and their variability. The modeling of survival has now a firm statistical basis and allows for a flexible analysis of the roles of environmental factors and of density[3]. The total variability of estimates of vital rates has different components, including sampling variability. A proper measure of the precision of survival estimates is therefore required to avoid confounding sampling variability and 'biological variability' due to intrinsic and extrinsic factors (Box 2). The same problem applies to estimates of population variability or trends[10]. Methods based on estimation of variance components should therefore be used to separate sampling variability from 'biological variability'.

Density dependence and vital rates in large herbivores

Fowler's review[11] supported Eberhardt's idea that vital rates have different sensitivities to changes in population density. In 21 species of large herbivores for which density dependence was reported, juvenile survival was involved in 15, age at first breeding in 12 and adult survival in only nine. Density dependence of adult reproductive traits was reported for 17 of 21 species, but measures of reproduction, such as the number of young per adult female, usually included early juvenile survival. Fowler[11] pointed out that differences in the response of vital rates to changes in population density were inconclusive because adult survival is far more difficult to assess than reproductive traits. Early recruitment can be measured by female:young ratios, but adult survival is very difficult to quantify without long-term monitoring of many marked individuals.

Recent studies based mainly on monitoring individually recognized animals also support Eberhardt's suggestion. Of nine species in which adult survival and other vital rates were studied in relation to variation in population density (Table 1), all exhibited density dependence in recruitment (juvenile survival, proportion of females breeding, or a combination of both traits), yearling survival was density-dependent in four, but only two island populations (Soay sheep and red deer) exhibited density dependence in adult survival. Even for these two species, survival of adult females varies much less than juvenile survival[12,13]. Therefore, juvenile survival is much more sensitive to density dependence than adult survival, which appears to be buffered against density effects.

Environmental variation and vital rates in large herbivores

Tables 2 and 3 summarize recent long-term studies on among-year variation in vital rates of large herbivores by focusing on juvenile survival (as a measure of recruitment) and survival of adult females. Whenever possible, we con-

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Box 1. The life cycle of female large herbivores: demographic analysis of a model population

Consider a population of large herbivores just before parturition. Suppose that each year 75% of 2-year-old females produce young [yearly proportion of 2-year-old females giving birth (%B2) = 0.75] and all females 3-year-old and older produce young [yearly proportion of 3-year-old and older females giving birth (%B3+) = 1]. All reproducing females give birth to a single offspring (litter size, LS = 1). This leads to a production of 0.5 females per breeding female assuming an even sex ratio at birth. Female offspring have a mean first-year survival of 0.50 (juvenile survival, SJ = 0.50) and a second-year survival of 0.75 (yearling survival, SY = 0.75). From 2 to 7 years, the annual survival of females is 0.90 (prime-age survival, SA = 0.90). Survival probability decreases to 0.70 for females older than 7 years (senescent survival, SS = 0.70).

A Leslie–Usher matrix model[2] for this population is therefore:

0	0.1875	0.1875	0.1875	0.1875	0.1875	0.1875	0.1875
0.75	0	0	0	0	0	0	0
0	0.90	0	0	0	0	0	0
0	0	0.90	0	0	0	0	0
0	0	0	0.90	0	0	0	0
0	0	0	0	0.90	0	0	0
0	0	0	0	0	0.90	0	0
0	0	0	0	0	0	0.90	0.70

From this matrix, we obtain a population multiplication rate (λ) of 1.026. The elasticities of different vital rates (i.e. the change of λ due to a given proportional change in a vital rate, a_{ij}) are defined by:

$$e_{ij} = \frac{\partial Ln(\lambda)}{\partial Ln(a_{ij})} = \frac{a_{ij}}{\lambda}\frac{\partial\lambda}{\partial a_{ij}}$$

For the above Leslie–Usher matrix, we obtain[2]:

$$e(\text{recruitment}) = 0.174$$

where parameters defining recruitment [SJ, LS, and (%B2 + %B3+)] all have the same elasticity because changing any of these parameters by a certain percentage will have exactly the same impact on λ (multiplicative terms in the Leslie matrix). Elasticities of %B2 and %B3+ were respectively 0.023 and 0.151.

$$e(SY) = 0.174$$
$$e(SA) = 0.513$$

where elasticity of prime-age survival is calculated as the sum of the elasticities of 5 year age classes (between 2 and 7 years of age).

$$e(SS) = 0.140$$

Variation in adult survival has the greatest effect on λ: a change in adult survival should have about three times more impact on λ than the equivalent change in recruitment.

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sidered only prime-aged adults (typically those aged 2–7 years[14,15], but including some older age classes in larger species like red deer[16]), because the survival of older individuals appears to be lower[14,15] and therefore estimates of 'adult' survival that include all age classes would be affected by population age structure. The survival of prime-aged females of 24 populations of 16 species of large herbivores monitored for a minimum of 5 years shows little among-year variation (coefficient of variation (CV) varying from 2 to 15%, Table 2). In contrast, juvenile survival shows marked temporal variation in 19 populations of 14 species (CV varying from 12 to 88%, Table 3). The differential response of adult and juvenile survival to environmental variation is clearly evident from a comparison of the same populations (numbered studies in Tables 2 and 3). In all 18 populations, yearly juvenile survival varied more than adult survival.

The high yearly variation in juvenile survival probably has multiple causes. Predation[17–20] drought in spring and summer[21,22] rainfall[23,24], harsh winters[17,19,21,23], low birth weight and early growth rates[12,19,23], late parturition[19,23], poor calving areas[25], lack of suitable bedding sites[19], genetic factors[23] and altered immunocompetence of neonates[26] have been reported to decrease juvenile survival in ungulates. Although almost as many causes of adult mortality have been reported,

Table 1. Evidence for/against density-dependent responses in vital rates of eight species of large herbivores

Species	Refs	Evidence for density-dependence in:	No evidence for density-dependence in:	Range of density (number/km²)
White-tailed deer (Odocoileus virginianus)	37	Juvenile survival in summer, reproductive success of 2 and 3 years old females and recruitment	Adult survival	14–26
Greater Kudu (Tragelaphus strepsiceros)	24	Juvenile survival in both populations studied, yearling survival in one population	Prime-age and senescent survival in both populations and yearling survival in one population	1.5–3 2.5–4
Roe deer (Capreolus capreolus)	14,22	Age at first breeding and juvenile survival in summer	Yearling, prime-age and senescent survival and fecundity	6–21
Red deer (Cervus elaphus scoticus)	13	Age at first breeding, fecundity of milk yield hinds, juvenile survival in winter, male yearling survival and adult survival	Summer part of juvenile survival, yearling survival of females and breeding proportion of prime age females	18–25
Wapiti (Cervus elaphus canadensis)	38,19	Juvenile survival	Adult survival	3–13.5
Bighorn sheep (Ovis canadensis)	39,15	Juvenile survival, age at first breeding and female yearling survival	Yearling male survival, prime-age and senescent survival	0.8–2.6ª
Reindeer (Rangifer tarandus)	40	Age at first breeding and recruitment	Breeding proportion of adult females and adult survival	0.5–5.5ᵇ
Donkey (Equus asinus)	41	Age at first breeding and juvenile survival	Breeding proportion of adult females and adult survival	1.5 and 3ᶜ
Soay sheep (Ovis aries)	12	Juvenile, yearling and adult survival	Fecundity	96–222

ªFemale density only.
ᵇDensity variation among contrasted populations.
ᶜDensity variation between two experimental sites.

including factors such as epizootics that caused significant yearly differences in adult survival[15,27], the available evidence indicates that, within a population, adult survival is always less variable than juvenile survival. This pattern is apparently independent of the main proximal causes of mortality and occurs in different taxa, in different continents and in widely different environments.
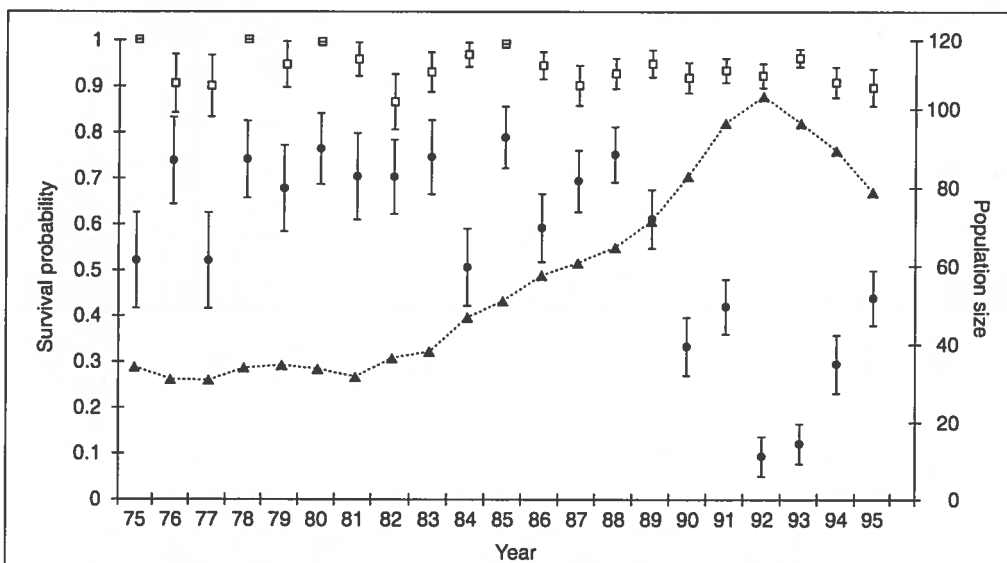
Juvenile survival, which determines recruitment, is highly sensitive to limiting factors, regardless of whether its variation is caused by changes in population density or by stochastic environmental factors. Adult female survival is buffered against most limiting factors (Fig. 1). Only long-term studies of a large sample of marked individuals can detect variation in survival of large herbivores (Box 2). A large sample is required to reduce sampling variability and many years of monitoring are required to measure variability in yearly survival, over a range of densities and environmental variation. In addition, it appears that estimates of adult survival of large herbivores are subject to greater sampling error than estimates of juvenile survival (Box 2). Therefore, analyses that partition biological and sampling variability will likely reinforce our conclusion that adult survival is much less variable than juvenile survival.

Fig. 1. An example of the contrasting variabilities in juvenile and prime-age adult survival in large herbivorous mammals: survival of bighorn sheep at Ram Mountain, Alberta, from 1975 to 1995[15,39]. Bars indicate SE. The number of females (dashed line) increased after 1981 and density effects on juvenile survival became evident after about 1988. Survival in 1975–1988 was mostly independent of population density. Black points, yearly estimates of juvenile survival; open squares, yearly estimates of prime age survival of females (2–7 years old).

Constant adult survival or variable recruitment: which is more important for population dynamics of large herbivores?

Many demographic analyses of large vertebrates have shown that adult survival has the highest elasticity, while juvenile survival and reproductive traits have the lowest elasticity[28,29] (Box 1). In general, elasticity of adult survival increases with generation length[30], which in turn increases with body

Table 2. Variation in prime-age adult survival of females in response to environmental stochasticity[a] in populations of large herbivores (with at least 5 years' monitoring)

Species	Refs	Mean survival	Min	Max	CV	N[b]	Methods[c]	Analysis[d]	Number of years
Mule deer (*Odocoileus hemionus*)	43	(1)[e] 0.856	0.692	1	0.101	741	CMR	DA	13
		(2) 0.807	0.743	0.899	0.070	634	CMR	DA	9
	17	(3) 0.875	0.760	1	0.090	185	RT	CR	6
Caribou/Reindeer (*Rangifer tarandus*)	25	0.842	0.750	0.930	0.088	538	RT	CR	10
	44	0.878[f]	0.810	0.950	0.058	532	RT	CR	9
	41	(4) 0.940[g]	0.920	0.963	0.017		CC	DA	6[g]
Greater Kudu (*Tragelaphus strepsiceros*)	24	(5) 0.933	0.810	1	0.061	7–57[h]	CMR	DA	11
		(6) 0.889	0.829	0.954	0.043	27–82[h]	CMR	DA	11
Bighorn sheep (*Ovis canadensis*)	15	(7) 0.956	0.871	1	0.033	872	CMR	CR	21
	(updated)	(8) 0.935	0.750	1	0.068	377	CMR	CR	12
Roe deer (*Capreolus capreolus*)	14	(9) 0.947	0.776	1	0.079	287	CMR	CR	10
	(updated)	(10) 0.942	0.797	1	0.077	302	CMR	CR	10
Soay sheep (*Ovis aries*)	12	(11) 0.871[i]	0.696	0.980	0.151	733	CMR	DA	6
Moose (*Alces alces*)	35	(12) 0.949	0.907	1	0.033	524	RT	CR	10
Red deer (*Cervus elaphus scoticus*)	16	(13) 0.955			0.077		CMR	DA	20
Mouflon (*Ovis gmelini*)	27 (updated)	0.841[j]	0.658	1	0.130	130	CMR	CR	7
Chamois (*Rupicapra rupicapra*)	44 (updated)	0.960					CMR	CR	6
Ibex (*Capra ibex*)	45 (updated)	0.965	0.709	1	0.086		CMR	CR	13
Dall sheep (*Ovis dalli*)	46	(14) 0.880	0.710	1	0.108		CC	DA	10
Wapiti (*Cervus elaphus canadensis*)	38	(15) 0.920					CC	DA	15
	47	0.892	0.778	1	0.117	46	RT	CR	5
Saïga (*Saiga tatarica*)	21	(16) 0.787[k]	0.680	0.810					
Pronghorn (*Antilocapra americana*)	J. Byers (pers. commun.)	(17) 0.978	0.850	1	0.041		CMR	DA	13
Mountain goat (*Oreamnos americanus*)	Unpubl. data	(18) 0.916	0.800	1	0.079	160	CMR	DA	7

[a]Environmental stochasticity includes here all sources of variation in the underlying vital rate. In particular, no effect was made to partition density-dependent from other variation. Then, our CVs include sampling variation as well as biological variation.

[b]Sample size: number of 'animal-years' used for estimating survival probabilities.

[c]CMR: monitoring of individually marked animals (using collars, ear tags or natural marks) by resighting or recaptures; RT: monitoring of individually marked animals by radiotelemetry; CC: monitoring using composition counts.

[d]CR: estimates based on capture–recapture modeling (see Ref. 3 for methods) accounting for capture probability less than 1; DA: direct assessment of survival from the proportion of individuals at risk known to have survived (assumes capture probability to be 1).

[e]Numbers in parentheses indicate populations for which juvenile survival was also available (see Table 3).

[f]Winter survival (November to May) only.

[g]Variation among contrasted populations.

[h]Assumed to represent the largest and smallest sample size for a given year.

[i]Winter mortality only.

[j]Prime-age females defined from 3 to 5 years of age.

[k]Methods and N not detailed in the original paper. Mean survival probability was obtained using the frequency of good and bad summer/winter conditions given in the paper.

size. These modeling results, however, do not rule out the possibility that all vital rates account for similar proportions of variance in population growth rate and therefore play similar roles in ungulate population dynamics. Some studies suggest that recruitment could be a stronger determinant of changes in population size than adult survival. Thus, juvenile survival was claimed to be the most important factor influencing population responses of peccary to fluctuating food availability[31].

Hatter and Janz[32] monitored a population of mule deer before, during and after a decline, and concluded that the highly variable juvenile survival (from 0.07 to 0.41) was more important than the constant adult survival (from 0.74 to 0.76) in explaining changes in population size. Gasaway et al.[33], on the other hand, suggested that high mortality among adults was the primary demographic process limiting ungulate populations in Etosha. Therefore, it appears that the roles of adult survival and recruitment on population dynamics of large herbivores cannot be assessed without further demographic analyses. Escos et al.[28] and Walsh et al.[29] underlined the difficulties of teasing apart the contributions of different vital rates to yearly changes in population size. Elasticity analyses alone cannot measure these contributions. To the theoretical estimates of what might happen (measured by elasticity) we must join empirical estimates of what happens (measured by long-term variability). This review has shown that adult survival is much less variable than juvenile survival. The next logical step will be to combine measurements of elasticity and variability to identify which vital rates are more important in causing changes in natural populations.

Prospects

In large herbivores, recruitment is the main target of limiting factors, both density-dependent and density-independent. Adult female survival appears buffered against temporal variation regardless of the causes of mortality, with

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Box 2. Assessing components of variability in stochastic environments

The variability of estimates of vital rates and population size is composed of sampling variability and biological ('true') variability[10]. The latter can be further partitioned in different components, such as intrinsic and extrinsic factors. To distinguish between sampling and biological variability we need a reliable measure of the sampling precision of estimates. For example, assuming a constant survival rate equal to 0.90 and estimating it by releasing each year 100 marked individuals results in a sampling standard error equal to $\sqrt{[p*(1-p)]/100} = 0.03$, and therefore observing estimates varying by ±5% may be due entirely to sampling variation. The variance $\sigma_{\hat{a}}^2$, of the estimator $\hat{a}$ of a vital rate, a, is the sum of the biological variance, σ_a^2, and the sampling variance, $var(\hat{a}|a)$. Methods based on estimation of variance components exist to separate sampling variability from biological variability[10,50].

The bias in the estimate of biological variance when ignoring sampling variance, as well as the precision of the estimate, depend on the size of both variance components, which are different for juvenile and adult survival (see Table below).

As a typical example of adult survival, we assume true survival rates equal to 0.85, 0.86, ..., 0.95, for an average survival of 0.90 and σ_a equal to 0.030. For juvenile survival, we assume that true survival rates are equal to 0.25, 0.30, ..., 0.75, for an average survival of 0.50 and σ_a equal to 0.158.

	Adult Survival			Juvenile Survival		
N	50	100	200	50	100	200
$\sigma_{\hat{a}}$	0.051	0.042	0.036	0.166	0.162	0.160
Relative Bias	70	40	20	5	2	1
SE ($\hat{\sigma}_a$)	0.015	0.010	0.006	0.022	0.015	0.010

The sampling precision increases with the number of animals released, N, and when survival rate is close to 1 (or 0). The relative bias when ignoring sampling precision, $(\sigma_{\hat{a}} - \sigma_a)/\sigma_a$ is then expected to be larger for adult survival than for juvenile survival (for a given N), but the precision of the estimate, $\hat{\sigma}_a$, is higher.

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the exception of disease. While this pattern is obvious from available case studies, our understanding of population dynamics in large herbivore populations suffers from a biased distribution of studies. First, reliable information exists for only 16 of about 250 extant species of large herbivores, a sampling intensity of 6%. More importantly, 15 of the 16 species are temperate ungulates, while most ungulate species occur in the tropics. We thus require detailed information about variability of vital rates for large tropical herbivores. Differences in seasonality and in predation pressure may well result in different population dynamics for temperate and tropical ungulates[33,34]. To establish how variation in demographic variables affects population size, however, we need more studies based on marked animals monitored over several years. Such studies will enable us to combine the observed temporal variation of a given vital rate with the calculated effect of a change in this vital rate (elasticity) to correctly assess the respective roles of recruitment and adult survival on population dynamics of large herbivores. Recent intensive radio-tracking studies have been particularly useful because they often obtained information on causes of death[17,19,35]. Knowledge of causes of death allows a better estimation of the impacts of different mortality factors.

Many long-term studies of population dynamics of large herbivores have relied almost exclusively on observational evidence. Experimental manipulations of population size[36] and of other ecological variables such as predation pressure would provide more reliable information. Manipulations would also provide data on the effects of population density or predation over a shorter time than observational studies. Ungulate populations that are subject to hunting or other forms of artificial control provide ideal opportunities for experimental tests of density dependence[17]. Predator control and predator reintroduction programs provide the opportunity to assess the role of predation. Therefore, cooperation among researchers and government agencies in long-term studies of ungulates is likely to advance our understanding of population ecology while providing useful information for conservation and management.

References
1 Caughley, G. (1977) *Analysis of Vertebrate Populations*, John Wiley & Sons
2 Tuljapurkar, S. and Caswell, H. (1997) *Structured-Population Models in Marine, Terrestrial, and Freshwater System*, Chapman & Hall
3 Lebreton, J.D. *et al.* (1993) **The statistical analysis of survival in animal populations**, *Trends Ecol. Evol.* 3, 91–95
4 Sæther, B.E. (1997) **Environmental stochasticity and population dynamics of large herbivores: a search for mechanisms**, *Trends Ecol. Evol.* 12, 143–149
5 Gaillard, J-M. *et al.* (1989) **An analysis of demographic tactics in birds and mammals**, *Oikos* 56, 59–76
6 Eberhardt, L.L. (1977) **Optimal management policies for marine mammals**, *Wildl. Soc. Bull.* 5, 162–169
7 Purvis, A. and Harvey, P.H. (1995) **Mammal life-history evolution: a comparative test of Charnov's model**, *J. Zool. Lond.* 237, 259–283
8 Menkens, G.E. and Boyce, M.S. (1993) **Comments on the use of time-specific and cohort life tables**, *Ecology* 74, 2164–2168
9 McCullough, D.R. *et al.* (1994) **Sources of inaccuracy in black-tailed deer herd composition counts**, *J. Wildl. Manage.* 58, 319–329
10 Link, W.A. and Nichols, J.D. (1994) **On the importance of sampling variance to investigations of temporal variation in animal population size**, *Oikos* 69, 539–544
11 Fowler, C.W. (1987) **A review of density dependence in populations of large mammals**, in *Current Mammalogy* (Genoways, H.H., ed.), pp. 401–441, Plenum Press
12 Clutton-Brock, T.H. *et al.* (1992) **Early development and population fluctuations in Soay sheep**, *J. Anim. Ecol.* 61, 381–396
13 Clutton-Brock, T.H. and Lonergan, M.E. (1994) **Culling regimes and sex ratio biases in Highland red deer**, *J. Appl. Ecol.* 31, 521–527
14 Gaillard, J-M. *et al.* (1993) **Roe deer survival patterns: a comparative analysis of contrasting populations**, *J. Anim. Ecol.* 62, 778–791
15 Jorgenson, J.T. *et al.* (1997) **Effects of age, sex, disease and density on survival of bighorn sheep**, *Ecology* 78, 1019–1032
16 Benton, T.G. *et al.* (1995) **Does environmental stochasticity matter? Analysis of red deer life-histories on Rhum**, *Evol. Ecol.* 9, 559–574
17 Bartmann, R.M. *et al.* (1992) **Compensatory mortality in a Colorado mule deer population**, *Wildl. Monogr.* 121, 1–39
18 Festa-Bianchet, M. *et al.* (1994) **Mountain goat recruitment: kid production and survival to breeding age**, *Can. J. Zool.* 72, 22–27
19 Singer, F.J. *et al.* (1997) **Density dependence, compensation, and environmental effects on elk calf mortality in Yellowstone National Park**, *J. Wildl. Manage.* 61, 12–25
20 Linnell, J.D.C. *et al.* (1995) **Who killed Bambi? The role of predation in the neonatal mortality of temperate ungulates**, *Wildl. Biol.* 1, 209–223
21 Milner-Gulland, E.J. (1994) **A population model for the management of the saiga antelope**, *J. Appl. Ecol.* 31, 25–39
22 Gaillard, J-M. *et al.* **Early survival in roe deer: causes and consequences of cohort variation in two contrasted populations**, *Oecologia* (in press)
23 Clutton-Brock, T.H. and Albon, S.D. (1989) *Red Deer in the Highlands*, Blackwell
24 Owen-Smith, N. (1990) **Demography of a large herbivore, the greater kudu *Tragelaphus strepsiceros*, in relation to rainfall**, *J. Anim. Ecol.* 59, 893–913

25 Fancy, S.G. *et al.* (1994) Demography of the Porcupine caribou herd, 1983–1992, *Can. J. Zool.* 72, 840–846

26 Sams, M.G. *et al.* (1996) Physiological correlates of neonatal mortality in an overpopulated herd of white-tailed deer, *J. Mamm.* 77, 179–190

27 Cransac, N. *et al.* Patterns of mouflon (*Ovis gmelini*) survival under moderate environmental conditions: effects of sex, age and epizootics, *Can. J. Zool.* (in press)

28 Escos, J. *et al.* (1994) Application of the stage-projection model with density-dependent fecundity to the population dynamics of Spanish ibex, *Can. J. Zool.* 72, 731–737

29 Walsh, N.E. *et al.* (1995) Evaluating growth of the Porcupine Caribou Herd using a stochastic model, *J. Wildl. Manage.* 59, 262–272

30 Lebreton, J.D. and Clobert, J. (1990) Bird population dynamics, management and conservation: the role of mathematical modeling, in *Bird Population Studies: Their Relevance to Conservation and Management* (Perrins, C.M., Lebreton, J.D. and Hirons, G.J.M., eds), pp. 105–125, Oxford University Press

31 Wilber, J.P. *et al.* (1991) Effects of seasonally varying diet quality on collared peccary population dynamics – a simulation study, *Ecol. Model.* 53, 109–129

32 Hatter, I.W. and Janz, D.W. (1994) Apparent demographic changes in black-tailed deer associated with wolf control on northern Vancouver Island, *Can. J. Zool.* 72, 878–884

33 Gasaway, W.C. *et al.* (1996) Persistent low densities of plains ungulates in Etosha National Park, Namibia: testing the food-regulating hypothesis, *Can. J. Zool.* 74, 1556–1572

34 Fryxell, J.M. (1987) Food limitation and demography of a migratory antelope, the white-eared kob, *Oecologia* 72, 83–91

35 Ballard, W.B. *et al.* (1991) Population dynamics of moose in South-central Alaska, *Wildl. Monogr.* 114, 1–49

36 Sinclair, A.R.E. (1989) Population regulation in animals, in *Ecological Concepts* (Cherrett, J.M., ed.), pp. 197–241, Blackwell Scientific Publications

37 Dusek, G.L. *et al.* (1989) Population ecology of white-tailed deer along the lower Yellowstone River, *Wildl. Monogr.* 104, 1–68

38 Coughenour, M.B. and Singer, F.J. (1996) Elk population processes in Yellowstone National Park under the policy of natural regulation, *Ecol. Appl.* 6, 573–593

39 Festa-Bianchet, M. *et al.* (1995) Life-history consequences of variation in age of primiparity in bighorn ewes, *Ecology* 76, 871–881

40 Skogland, T. (1985) The effects of density-dependent resource limitations on the demography of wild reindeer, *J. Anim. Ecol.* 54, 359–374

41 Choquenot, D. (1991) Density-dependent growth, body condition, and demography in feral donkeys: testing the food hypothesis, *Ecology* 72, 805–813

42 Pac, D.F. *et al.* (1991) *Mule Deer Population Organization, Behavior and Dynamics in a Rocky Mountain Environment*, Montana Department of Fish, Wildlife & Park

43 Crête, M. *et al.* (1996) Relative contribution of decreased productivity and survival to recent changes in the demographic trend of the Rivière George Caribou Herd, *Rangifer* 9, 27–36

44 Loison, A. *et al.* (1994) New insight on survivorship of female chamois (*Rupicapra rupicapra*) from marked animals, *Can. J. Zool.* 72, 591–597

45 Toïgo, C. *et al.* (1997) Adult survival of the sexually dimorphic Alpine ibex (*Capra ibex ibex*), *Can. J. Zool.* 75, 75–79

46 Hoefs, M. and Bayer, M. (1983) Demographic characteristics of an unhunted Dall sheep (*Ovis dalli*) population in southwest Yukon, Canada, *Can. J. Zool.* 61, 1346–1357

47 Unsworth, J.W. *et al.* (1993) Elk mortality in the Clearwater drainage of Northcentral Idaho, *J. Wildl. Manage.* 57, 495–502

48 Jorgenson, J.T. *et al.* (1993) Harvesting bighorn ewes: consequences for population size and trophy ram production, *J. Wildl. Manage.* 57, 429–435

49 Clutton-Brock, T.H. *et al.* (1987) Interactions between population density and maternal characteristics affecting fecundity and juvenile survival in red deer, *J. Anim. Ecol.* 56, 857–871

50 Burnham, K.P. *et al.* (1987) *Design and Analysis Methods for Fish Survival Experiments Based on Release–Recapture*, American Fisheries Society Monograph 5, Bethesda

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21 Brown, J.H. (1984) **On the relationship between abundance and distribution of species**, *Am. Nat.* 124, 255–279

22 Pulliam, H.R. (1988) **Sources, sinks, and population regulation**, *Am. Nat.* 132, 652–661

23 Lennon, J.J., Turner, J.R.G. and Connell, D. (1997) **A metapopulation model of species boundaries**, *Oikos* 78, 486–502

24 Dennis, B. (1989) **Allee effects: population growth, critical density, and the chance of extinction**, *Nat. Res. Model.* 3, 481–538

25 Hopf, F.A. and Hopf, F.W. (1985) **The role of the Allee effect in species packing**, *Theor. Popul. Biol.* 27, 27–50

26 Gruntfest, Y., Arditi, R. and Dombrovsky, Y. (1997) **A fragmented population in a varying environment**, *J. Theor. Biol.* 185, 539–547

27 Lande, R., Engen, S. and Sæther, B.E. (1998) **Extinction times in finite metapopulation models with stochastic local dynamics**, *Oikos* 83, 383–389

28 Kindvall, O. *et al.* (1998) **Individual mobility prevents an Allee effect in sparse populations of the bush cricket *Metrioptera roeseli*: an experimental study**, *Oikos* 81, 449–457

29 Stacey, P.B. and Taper, M. (1992) **Environmental variation and the persistence of small populations**, *Ecol. Appl.* 2, 18–29

30 Halliday, T.R. (1980) **The extinction of the passenger pigeon *Ectopistes migratorius* and its relevance to contemporary conservation**, *Biol. Conserv.* 17, 157–162

31 Bucher, E.H. (1992) **The causes of extinction of the passenger pigeon**, *Current Ornithol.* 9, 1–36

32 Reed, J.M. (1999) **The role of behavior in recent avian extinctions and endangerments**, *Conserv. Biol.* 13, 232–241

33 Sillero-Zubiri, C., King, A.A. and Macdonald, D.W. (1996) **Rabies and mortality in Ethiopian wolves (*Canis simensis*)**, *J. Wildl. Dis.* 32, 80–86

34 Alvarez, L.H.R. (1998) **Optimal harvesting under stochastic fluctuations and critical depensation**, *Math. Biosci.* 152, 63–85

35 Allee, W.C. (1938) *The Social Life of Animals*, William Heinemann

36 Lande, R., Engen, S. and Sæther, B.E. (1994) **Optimal harvesting, economic discounting and extinction risk in fluctuating populations**, *Nature* 372, 88–90

37 Myers, R.A. *et al.* (1995) **Population dynamics of exploited fish stocks at low population levels**, *Science* 269, 1106–1108

38 Liermann, M. and Hilborn, R. (1997) **Depensation in fish stocks: a hierarchic Bayesian meta-analysis**, *Can. J. Fish. Aquat. Sci.* 54, 1976–1984

39 Lewis, M.A. and Kareiva, P. (1993) **Allee dynamics and the spread of invading organisms**, *Theor. Popul. Biol.* 43, 141–158

40 Veit, R.R. and Lewis, M.A. (1996) **Dispersal, population growth, and the Allee effect: dynamics of the house finch invasion of eastern North America**, *Am. Nat.* 148, 255–274

41 Hopper, K.R. and Roush, R.T. (1993) **Mate finding, dispersal, number released, and the success of biological-control introductions**, *Ecol. Entomol.* 18, 321–331

42 Green, R.E. (1997) **The influence of numbers released on the outcome of attempts to introduce exotic bird species to New Zealand**, *J. Anim. Ecol.* 66, 25–35

43 Soderquist, T.R. (1994) **The importance of hypothesis testing in reintroduction biology: examples from the reintroduction of the carnivorous marsupial *Phascogale tapoatafa***, in *Reintroduction Biology of Australian and New Zealand Fauna* (Serena, M., ed.), pp. 156–164, Surrey Beaty and Sons

44 Boyce, M.S. (1992) **Population viability analysis**, *Annu. Rev. Ecol. Syst.* 23, 481–506

45 Stephens, P.A., Sutherland, W.J. and Freckleton, R.P. **What is the Allee effect?** *Oikos* (in press)

46 Côté, I.M. and Gross, M.R. (1993) **Reduced disease in offspring: a benefit of coloniality in sunfish**, *Behav. Ecol. Sociobiol.* 33, 269–274

47 Donaldson, J.S. (1993) **Mast-seeding in the cycad genus *Encephalartos* – a test of the predator satiation hypothesis**, *Oecologia* 94, 262–271

48 Ferson, S. and Burgman, M.A. (1990) **The dangers of being few: demographic risk analysis for rare species extinction**, *Ecosystem Management: Rare Species and Significant Habitats. New York State Museum Bulletin* 471, 129–132

49 Sussman, R.W. and Garber, P.A. (1987) **A new interpretation of the social organisation and mating system of the Callitrichidae**, *Int. J. Primatol.* 8, 73–92

Inverse density dependence and the Allee effect

Franck Courchamp
Tim Clutton-Brock
Bryan Grenfell

The Allee effect describes a scenario in which populations at low numbers are affected by a positive relationship between population growth rate and density, which increases their likelihood of extinction. The importance of this dynamic process in ecology has been under-appreciated and recent evidence now suggests that it might have an impact on the population dynamics of many plant and animal species. Studies of the causal mechanisms generating Allee effects in small populations could provide a key to understanding their dynamics.

Franck Courchamp, Tim Clutton-Brock and Bryan Grenfell are at the Dept of Zoology, University of Cambridge, Downing Street, Cambridge, UK CB2 3EJ (fc219@cam.ac.uk; thcb@hermes.cam.ac.uk; bryan@zoo.cam.ac.uk).

In 1931, Warder Clyde Allee proposed that intraspecific cooperation might lead to inverse density dependence, an idea that he later extended in his famous 1949 book on animal ecology[1]. Exactly half a century later, it is timely to review the influence of his concept on current ecological research, and assess future prospects. Allee observed that many animal and plant species suffer a decrease of the per capita rate of increase as their populations reach small sizes or low densities (Fig. 1). Under such conditions, the rate of increase can reach zero, or even negative values, because of a decrease in reproduction and/or survival when con-specific individuals are not numerous enough: 'undercrowding, as well as over-crowding, may be limiting' (Box 1). One of Allee's collaborators, E.P. Odum, first referred to this process as Allee's Principle[2], but it is now generally known as the Allee effect.

Causes of inverse density dependence

The Allee effect strictly refers to inverse density dependence at low density. Factors involved in generating inverse density dependence are numerous and have been described for most major animal taxa[3]. These factors can be classified into three main categories[4]. The first is genetic inbreeding and loss of heterozygosity, leading to decreased fitness (such as demonstrated for plants[5,6]). The second is demographic stochasticity (including sex-ratio fluctuations)[4], as illustrated by the failure of many biological control programmes that released control insects in too small numbers. Another example concerns threatened species with low fecundity and small population size, such as the Kakapo *Strigops habroptilus*, the world's largest parrot (Fig. 2). In 1997, the total population of this flightless bird consisted of 54 individuals, of which only 20 were female (with few of these being
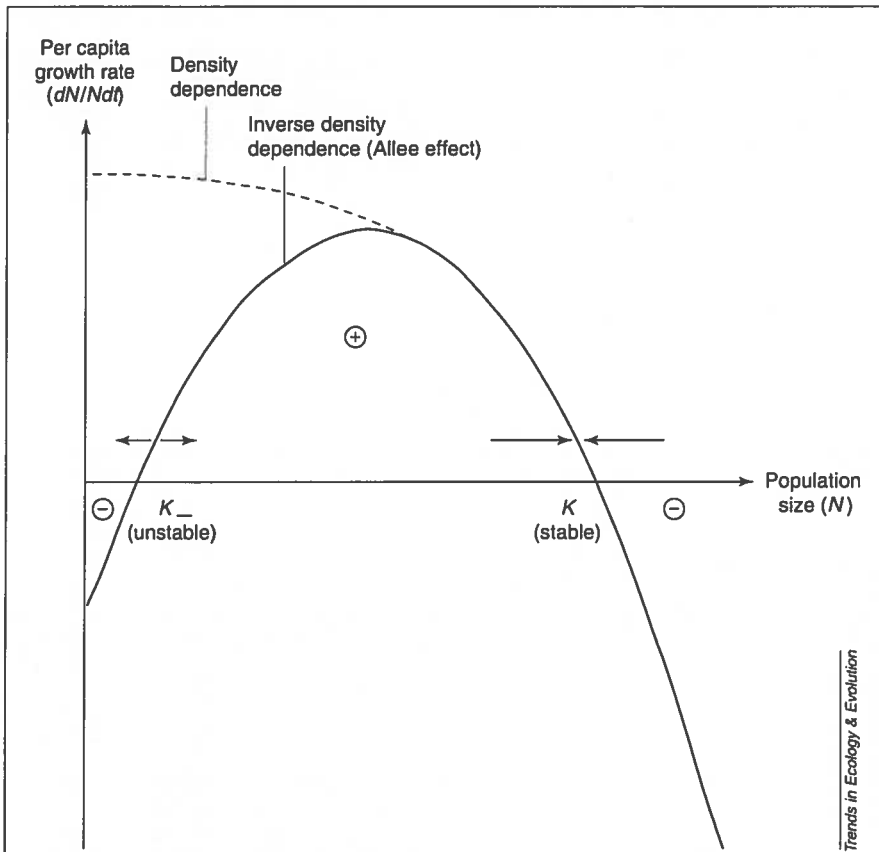
Fig. 1. Illustration of the Allee effect, from a very simple mathematical model of population dynamics:

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right)\left(\frac{N}{K_-} - 1\right)$$

The per capita growth rate (dN/dt) is negative above the carrying capacity (K) and positive below. However, in the presence of an Allee effect, it also decreases below a given population size, and can even become negative below a critical population threshold (K_-). When a population displaying this type of population dynamics is driven below the critical threshold, the low, sometimes negative, per capita growth rate may lead it to extinction.

Box 1. The floury little world of the *Tribolium*

One of the earliest illustrations of Allee's ideas of the existence of an optimal population size concerns his analysis of the laboratory work of three different researchers on the flour beetle, *Tribolium confusum*[35]. This species showed the 'most rapid population growth at an intermediate population size rather than with too few or too many present', as shown in his figure, reproduced below.
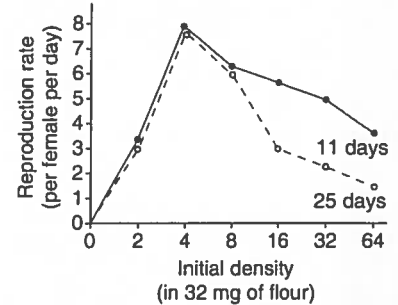
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(Online: Fig. I)

The higher growth rate at an intermediate population size was interpreted as the result of the interaction between two opposing processes. On one hand, 'adult beetles roam at random through their floury universe. They eat the flour, but they also eat their own eggs as they encounter these on their travels'[35]. Because of this, eggs are less likely to escape oophagy at high densities. However, females lay more eggs, and eggs with a higher percentage of fertility, when they have been stimulated by successive copulation, which is more likely to occur at high densities. As a result, there is an intermediate optimal population density, above the possible minimum one, in which the growth rate is higher than at lower or higher population densities. Later, Allee and collaborators[35] showed that fish are better able to survive water poisoning if other fish had previously lived in it, because their secretions had conditioned the environment. This relationship between fitness and density was, however, positive only until competition became the principal factor influencing population dynamics. Such an interaction between two processes with an opposing relationship to density is a reasonably general feature of the Allee effect.

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fertile), distributed across four islands[7]. A recent breeding program has resulted in the birth of nine chicks, but only two of these are female (R. Dennett, pers. commun.). The third category concerns the reduction in cooperative interactions when there are fewer individuals.

This last mechanism has attracted most research effort, probably partly because Allee himself proposed it, referring to it as 'proto-cooperation' or 'facilitation'[1]. Given that cooperation usually implies active participation, we prefer to use the more generalist term of facilitation, except for particular cases. Shortage of receptive mate encounters during the mating period when density is too low[8] is the most cited factor, although it represents only a small subset of social causes of inverse density dependence. Species in which fitness is enhanced by any type of conspecific facilitation might suffer from reduced density when intraspecific competitive processes are of secondary impor-

tance (Box 2). In this context, facilitation is taken in the broadest sense and sometimes includes sexual reproduction (where two organisms can be seen as 'cooperating' to pass on their genes to the next generation).

For example, decreased sexual reproduction owing to a lower probability of finding a mate at very low densities might generate a lower rate of recruitment, which in turn lowers the probability of finding mates in the next generation, thereby creating an extinction vortex, and ultimately the collapse of the population. Additionally, in cooperative animals, reduced recruitment may also be caused by higher juvenile mortality, owing to the cost of feeding or baby-sitting in small groups[9] as in suricates, *Suricata suricatta*.

The Allee effect might also be generated by lower survival, such as when antipredator strategies become inefficient in small groups of prey. Examples of this include the passive protection of

sea urchin larvae sheltered by adult spine canopies[10], the early warning or confusion effects in fish schools and ungulate herds[11], or more active sentinel systems or defence strategies, as in suricates[12]. However, because the extent of facilitation and/or cooperation might determine the strength of the Allee effect, many of these processes could be rather weak unless the populations are at very low density. In contrast, obligate cooperatively breeding species might experience a strong inverse density dependence, even when close to the carrying capacity, and may suffer from an Allee effect for most of their normal density range[12,13].
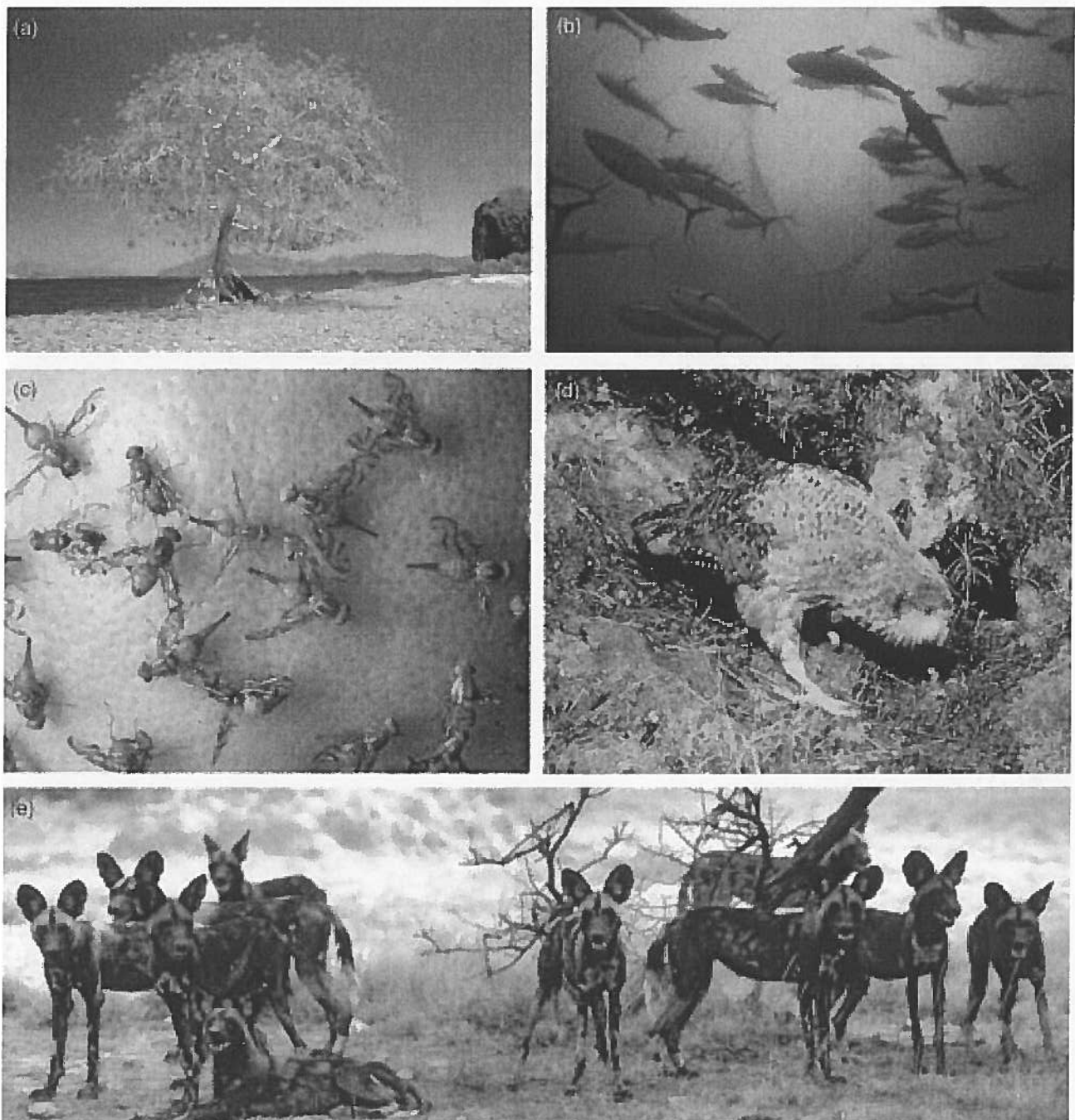
Fig. 2. Examples of the Allee effect in different taxa. (a) Because of a shortage of fertilization or of mating encounters, Allee effects can cause species extinction when density is too low. This is illustrated by pollination in fig trees (*Ficus* sp.), where small dispersed patches attract fewer pollinators or dispersers (*photo reproduced, with permission, from Corbis/C. Mattison*). (b) The Allee effect is important in group living animals, such as schooling fishes (here bluefin tunas *Thunnus thynnus* in fishing nets). It may also cause a population to collapse if harvesting pressure is too strong, as has happened for fisheries (*photo reproduced, with permission, from Corbis/J.L. Rotman*). (c) Because fruit flies attack more than 400 crops worldwide, they are considered to be one of the worst insect pests of agriculture. One of the techniques used to control them is the release of sterile males to create an Allee effect, as for these fruit flies, *Anastrepha ludens* (*photo reproduced, with permission, from J. Dykinga, Agricultural Research Service, USDA*). Another technique is to release natural enemies, in numbers large enough to ensure the Allee effect is avoided. (d) At very small population sizes, some endangered species, such as the Kakapo (*Strigops habroptilus*), have a low probability of finding receptive mates, and/or have a biased sex-ratio because of demographic stochasticity. There are only 54 individuals surviving of this giant parrot (*photo reproduced, with permission, from D. Merton*). (e) Obligate cooperative breeders, such as African wild dogs (*Lycaon pictus*), may have a critical group size below which the group would be very likely to go extinct (*photo reproduced, with permission, from J. Ginsberg*).

Implications for population dynamics

For all these phenomena, and others, the major consequence of the Allee effect is the existence of a critical density below which the aggregation unit considered (e.g. population, colony or social group) is likely to go extinct. This has been shown theoretically both with deterministic and stochastic mathematical models[4,13,14], and although still scarce, empirical evidence exists from very diverse ecological systems (Box 2). Because the mechanism is quite straightforward, very basic population dynamic models (comparable in simplicity to the classical Verlhust logistic equation) can be used to mimic the Allee effect (Fig. 1).

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Box 2. Allee effects, facilitation and cooperation

The Allee effect can be generated by a shortage of interactions among conspecifics at low density. These interactions range from strict cooperation to unconscious facilitation. At one extreme, strong cooperation, are taxa that form colonies (with different degrees of coloniality). For example, because offspring survival to maturity increases with colony size, the lifetime reproductive success of female social spiders, *Anelosimus eximius*, decreases in small colonies[36]. Smaller colonies of reef-building coral populations are less likely to survive attacks by mucilage coverage[37] or catastrophic climatic events[33]. In Damaraland mole-rats, *Cryptomys damarensis*, small colonies are more likely to fail because the colony work force is of insufficient size to locate food[38]. In plants, lower survival can be caused by a lack of conditioning effects at low densities[39], and some colonial seabirds need a critical density to establish and reproduce[1,40].

At the other extreme of sociality are individuals of species whose only form of contact with conspecifics is for sexual reproduction (which can in this context be considered as proto-cooperation). They can also be subject to Allee effects. For example, pollination of many species of plants (especially by animal vectors), is less efficient when inter-individual distances become too large or patches too small[39,41,42]. Fertilization in benthic invertebrates with free-spawn gametes, or with planktonic larvae, has also been shown to be insufficient at low population densities[33]. A shortage of encounters with receptive mates during the mating period[8] can increase the threat to small populations, such as those of the Glanville fritillary butterfly, *Melitaea cinxia*[18], and the northern spotted owl, *Strix occidentalis*[43]. An Allee effect may also delay the beginning of an invasion[32], or even prevent its success, as seen in the House Finch, *Carpodacus mexicanus*, in North America. The same is true for species introductions (for their conservation or for biological control of another species), which generally require repeated releases of large numbers of individuals before successful establishment[44,45].

Between these two extremes, the atypical social system of obligate cooperative breeders can generate an Allee effect, potentially responsible for their high rates of group extinction[13] (Box 3).

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The implications of the Allee effect are potentially very important in most areas of ecology[15] and evolution[14], but we will focus here on population dynamics only. As we will see below, the practical management of population numbers, whether aiming to increase or reduce them, is strongly affected by this effect. The consequences of Allee effects are also likely to be significant for the theory of population dynamics, because most classic models imply a linear decrease of growth with density, as opposed to the non-linear relationship associated with the Allee effect[14]. Similarly, current mathematical models seem to overestimate persistence times for metapopulations of species exhibiting an Allee effect, because even when explicitly considering small metapopulation sizes, they carry the implicit assumption that local populations always increase to their carrying capacity[16]. Other types of Allee effects have been demonstrated at the theoretical metapopulation level when the spatial dimension and stochasticity are taken into account[4,17]. The importance of the Allee effect in metapopulation dynamics has also been shown empirically, as for the endangered Glanville fritillary butterfly (*Melitaea cinxia*)[18].

Repercussions across trophic levels

Although it is an intraspecific phenomenon, some interspecific relationships are strongly influenced by the Allee effect. It is well known that smaller groups of prey may be more exposed to predation than larger groups[11]. It has also been shown, both theoretically and empirically, that if a species is a secondary prey item of a predator with a type II functional response, its death rate from predation will be inverse density dependent[19]. Similarly, the rate of infection for many parasitoid species has been shown to decrease with increasing host density[20]. Other interspecific relationships, such as nest parasitism[21] and kleptoparasitism[22] can also be affected (Box 3).

The victims of interspecific relationships (e.g. prey or hosts) are not the only ones prone to the Allee effect: at low density, their natural enemies can also suffer inverse density dependence. Indeed, some cooperative hunters are not as efficient if they have a small hunting party, because some prey require a certain number of individual hunters if they are to be successfully isolated and attacked[23,24] (Box 3). Other examples include kleptoparasites: hyenas (*Crocuta crocuta*) form large clans that spread out in search of prey and regroup once individuals have located a fresh kill and signalled to the others. A critical threshold in the clan size of hyenas is thus likely to limit the success of this type of foraging strategy when prey are scarce. This also seems to be true for many birds (whether predatory or not) regrouping in flocks to maximize resource location efficiency. In addition, it is reasonable to predict that inverse density-dependent mechanisms are likely to affect strongly the population dynamics of species such as parasitoids[20], because the difficulty of finding a mate at low densities compounds that of finding a host when the host density is also low.

Perhaps among the best known manifestations of population thresholds for extinction are some infectious pathogens, which do not persist below a critical host population size, as shown for human[25] as well as wildlife populations[26]. This is because the life history of some pathogens (mostly their rates of transmission and induced mortality) makes it difficult for them to infect new hosts before dying out if the host density is too low. Although this is not an Allee effect *per se*, this critical community size, which can take different mathematical forms according to the system modelled[27], has interesting analogies with minimum viable populations and extinction thresholds generated by inverse density dependence. At a different scale, too few parasites (either micro- or macroparasites) in a host are less likely to overcome the host's immune defence, resulting in the extinction of the

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Box 3. The Allee effect in African wild dogs?

It has recently been proposed that the high rates of group extinction observed in obligate cooperative breeders are generated by a need for a critical number of helpers, which produce an Allee effect[13]. As a result, a social group driven below a critical threshold would have a lower chance of recovery and consequently become even smaller, with an increasing risk of extinction.

This can be illustrated by the African wild dog, *Lycaon pictus*, which is currently facing the threat of extinction throughout its remaining geographical range. Many causes have been proposed to explain its current decline, including human persecution, diseases, habitat fragmentation and competition with other predators[46]. Although it has never been proposed, another, nonexclusive, factor is the existence of an Allee effect, which would render this species more sensitive to other mortality factors. Wild dogs live in groups of up to 20 adults and their dependent young[23]. The hunting strategy of the group usually requires a critical size to be energetically efficient[23,24,47]. A threshold group size might also be required for hunting because of kleptoparasitism by hyenas, which can be energetically very costly to small groups of wild dogs[22,47,48]. In addition, helpers are required by the breeding female: litters are very large (up to 20 pups), and the breeding female, then the pups, need to be fed by other members of the group[46,49]. Group members also help by chasing predators from the den area, and by staying at the den to protect the pups while the pack is hunting[46,49].

Consequently, a critical number of helpers might be needed for wild dog groups to survive. It has been suggested that groups of less than four adults are unable to reproduce successfully[46]. Furthermore, the impact of environmental stochasticity (including random catastrophes, such as droughts and epidemics) and of natural enemies (competitors, predators, kleptoparasites) might increase the extinction probability of cooperators by driving them closer to or below the critical threshold. Human activities and pathogens might act in the same way, increasing the threat of the Allee effect by decreasing group sizes. For example, because of high contact rates owing to wild dogs' social structure, a virus can probably spread rapidly among group members. The disease-induced death of several dogs might then reduce the group to insufficient size for survival.

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parasite. Consequently, there might be a critical threshold for many internal parasites.

Allee effects in more complex interspecific relationships, involving more than two species, have seldom been considered. However, given what is already known about the importance of this process on 'simple' competitive, predatory or parasitic relationships, it is reasonable to predict that models of processes such as predator- or parasite-mediated competition (which is an important ecological process[28]) will generate different outcomes in the presence of inverse density dependence. At the niche scale, the Allee effect can prevent persistence of plants that ameliorate physically stressful habitats[29]. This environmental conditioning is also important for many associated plant and animal species because it allows new colonization. At a larger scale, the Allee effect is likely to have a detectable influence on plant community dynamics and vegetation succession[29]. It is very likely that species are affected by inverse density dependence generated by a combination of all these ecological forces. Even those species displaying no obvious Allee effect can be affected by others that do, which means that most species are probably influenced, either directly or indirectly, by this dynamic process.

Implications for applied ecology

Species subjected to a strong Allee effect might be more susceptible to catastrophic population collapses with only a slight increase in mortality, resulting either from harvesting or 'natural' causes. Two generally conflicting interests in ecosystem management, long-term optimal harvesting and biodiversity preservation, which both aim to prevent these collapses, have much to gain from acknowledging potential Allee effects. In fisheries, for example, the existence of multiple equilibria has been recognized (in theory at least), and the existence of a critical threshold for harvested populations has been advanced as a highly plausible explanation for the collapse of fisheries in several parts of the world[30] (Fig. 2). As exploited fish species are usually schooling species, and a large school is generally considered to be a defence against predators[21], one should expect (and therefore attempt to prevent) Allee effects in these species.

Prevention of population collapses is also a priority in conservation biology[15], where it is widely admitted that populations of small size are often at greater risk of extinction. However, even though many conservation programs (including reintroduction) focus on the extinction risks encountered by very small populations, and the existence of a minimum population size below which they cannot recover, the Allee effect is still seldom taken into account in this area[15]. That the Allee effect is indexed in only five out of 35 of the most recent major books on conservation biology illustrates this deficiency very well. Other research areas where the Allee effect plays a critical role are ecosystem invasions[31,32] (Box 2) and, most importantly, biological control (Box 4).

What prospects for the Allee effect?

The early studies of population biology have been largely dominated by the importance of (negative) density dependence at high densities. In a time when anthropogenic disturbance has driven many populations to small sizes and/or low densities, we must now focus on the other extreme of population sizes. Indeed, studies demonstrating Allee effects and determining their causal mechanisms, either theoretically or empirically, ought to be more numerous in the future. There is a range of logistical problems associated with the study of very small natural populations, especially of mobile animals, rendering it difficult to demonstrate an Allee effect[14,18,21]. Nevertheless, in several different areas of ecology, empirical evidence is needed on this still poorly documented but nonetheless important dynamic process.

With the notable exception of biological control, which provides excellent opportunities to study experimentally the effect of population size on establishment and persistence, experimental studies of the Allee effect are both impractical and unethical in natural conditions. Therefore, one has either to rely on 'natural experiments', such as catastrophic events[33], or to work on laboratory populations[1], which can compensate for the lack of replicability and control typical of 'natural experiments'. Although they are less scarce than empirical studies, theoretical studies of the consequences of the Allee effect are also needed, especially concerning the dynamics of interspecific relationships.

Future progress in understanding the dynamics of small populations will most likely be achieved by creatively combining these different scientific approaches.

Knowing a given species is prone to a strong Allee effect would not be of much help if the population collapse was inevitable. In many cases, however, it should be possible to artificially reverse the fate of a population that is dangerously close to, or even below, its critical threshold. For example, densities of some plants or trees could be increased by dispersing seeds, or by planting individuals obtained from nurseries or from other, more dense populations. Similarly, social groups of some endangered vertebrates could be artificially increased (e.g. during a short period of captivity), thereby avoiding the loss of the smallest groups. More importantly, knowing that an Allee effect threatens a given population would allow the redirection of harvesting pressure towards less threatened populations. Similarly, protection efforts for an endangered species, if proven sensitive to the Allee effect, should be redefined according to different priorities: for many species, density as much as population size should become a criterion of endangerment in conservation programmes. As the causes of decline of many populations still remain a puzzle (as for the recent amphibian declines[34]), a more systematic investigation of potential Allee effects in endangered populations could be crucial to the better understanding of their dynamics, as well as efficiently protecting them against formally identified threats.

Box 4. Biological control: helped and hindered by Allee effects

The primary aim of biological control, which is nothing more than a planned biological invasion to get rid of another invasion, is to minimize the establishment and persistence of pests and maximize that of their enemies. This is one of the few research areas in which the Allee effect is plainly recognized and fully used. The first successful attempts at biologically controlling a pest insect to meet with success artificially created an Allee effect in the pest population by inundating it with sterile males[50]. This method is still widely used[50], as illustrated by the massive releases of sterile male Mediterranean fruit flies, *Ceratitis capitata*, last year in the USA. The emerging new concept of mammal control through virus-vectored immunocontraception[51] is likely to succeed because it should create an Allee effect.

An important issue in biological control programmes (and in the reintroduction of threatened species) concerns the minimum number of individuals that should be released to ensure the establishment of populations of natural enemies of the pest. Indeed, insufficient reproduction at low densities would result in a collapse of these populations because of at least two mechanisms[44]. First, the low probability at finding a mate at low density may lead to a lack of recruitment[8]. Second, in arrhenotokous insect species (when virgin females produce only males), failure to mate may result in a male-biased sex ratio, and therefore in demographic stochasticity[4]. Both potentially create an Allee effect, and both can result in the failure of the introduction[44].

PERSPECTIVES

References

1 Allee, W.C. *et al.* (1949) *Principles of Animal Ecology*, Saunders

2 Odum, P.E. (1959) *Fundamentals of Ecology*, Saunders

3 Fowler, C.W. and Baker, J.D. (1991) A review of animal population dynamics at extremely reduced population levels, *Report to the International Whaling Commission* 41, 545–554

4 Lande, R. (1998) Demographic stochasticity and Allee effect on a scale with isotropic noise, *Oikos* 83, 353–358

5 Lamont, B.B., Klinkhamer, P.G.L. and Witkowski, E.T.F. (1993) Population fragmentation may reduce fertility to zero in *Banksia goodii* – a demonstration of the Allee effect, *Oecologia* 94, 446–450

6 Fischer, M. and Matthies, D. (1998) RAPD variation in relation to population size and plant fitness in the rare *Gentianella germanica* (Gentianaceae), *Am. J. Bot.* 85, 811–819

7 Clout, M.N. and Merton, D.V. (1998) Saving the Kakapo: the conservation of the world's most peculiar parrot, *Bird Cons. Int.* 8, 281–296

8 Wells, H. *et al.* (1998) Mate location, population growth and species extinction, *Biol. Conserv.* 86, 317–324

9 Clutton-Brock, T.H. *et al.* (1998) Cost of cooperative behaviour in suricates (*Suricata suricatta*), *Proc. R. Soc. London Ser. B* 265, 185–190

10 Quinn, J.F., Wing, S.R. and Botsford, L.W. (1993) Harvest refugia in marine invertebrate fisheries – models and applications to the Red Sea urchin, *Strongylocentrotus franciscanus*, *Am. Zool.* 33, 537–550

11 Crawley, M.J., ed. (1992) *Natural Enemies, the Population Biology of Predators, Parasites and Diseases*, Blackwell

12 Clutton-Brock, T.H. *et al.* (1999) Predation, group size and mortality in a cooperative mongoose, *Suricata suricatta*, *J. Anim. Ecol.* 68, 672–683

13 Courchamp, F., Grenfell, B. and Clutton-Brock, T.H. (1999) Population dynamics of obligate cooperators, *Proc. R. Soc. London Ser. B* 266, 557–564

14 Dennis, B. (1989) Allee effects: population growth, critical density and the chance of extinction, *Nat. Res. Model.* 3, 481–538

15 Stephens, P.A. and Sutherland, W.J. (1999) Consequences of the Allee effect for behaviour, ecology and conservation, *Trends Ecol. Evol.* 14, 401–405

16 Amarasekare, P. (1998) Allee effects in metapopulation dynamics, *Am. Nat.* 152, 298–302

17 Lande, R. (1987) Extinction thresholds in demographic models of territorial populations, *Am. Nat.* 130, 624–635

18 Kuussaari, M. *et al.* (1998) Allee effect and population dynamics in the Glanville fritillary butterfly, *Oikos* 82, 384–392

19 Sinclair, A.R.E. *et al.* (1998) Predicting effects of predation on conservation of endangered prey, *Conserv. Biol.* 12, 564–575

20 Stiling, P.D. (1987) The frequency of density dependence in insect host–parasitoid systems, *Ecology* 68, 844–856

21 Sæther, B.E., Ringsby, T.H. and Röskaft, E. (1996) Life history variation, population processes and priorities in species conservation: towards a reunion of research paradigms, *Oikos* 77, 217–226

22 Carbone, C., DuToit, J.T. and Gordon, I.J. (1997) Feeding success in African wild dogs: does kleptoparasitism by spotted hyenas influence hunting group size? *J. Anim. Ecol.* 66, 318–326

23 Creel, S. and Creel, N.M. (1995) Communal hunting and pack size in african wild dogs, *Lycaon pictus*, *Anim. Behav.* 50, 1325–1339

24 Creel, S. (1997) Cooperative hunting and group size: assumptions and currencies, *Anim. Behav.* 54, 1319–1324

25 Keeling, M.J. and Grenfell, B.T. (1997) Disease extinction and community size: Modelling the persistence of measles, *Science* 275, 65–67

26 Swinton, J. *et al.* (1998) Persistence thresholds for phocine distemper virus infection in harbour seal *Phoca vitulina* metapopulations, *J. Anim. Ecol.* 67, 54–68

27 Grenfell, B. and Harwood, J. (1997) (Meta)population dynamics of infectious diseases, *Trends Ecol. Evol.* 12, 395–399

28 Hudson, P. and Greenman, J. (1998) Competition mediated by parasites: biological and theoretical progress, *Trends Ecol. Evol.* 13, 387–390

29 Bertness, M.D. and Leonard, G.H. (1997) The role of positive interactions in communities: lessons from intertidal habitats, *Ecology* 78, 1976–1989

30 Roughgarden, J. and Smith, F. (1996) Why fisheries collapse and what to do about it, *Proc. Natl. Acad. Sci. U. S. A.* 93, 5078–5083

31 Lewis, M.A. and Kareiva, P. (1993) Allee dynamics and the spread of invading organisms, *Theor. Popul. Biol.* 43, 141–158

32 Veit, R.R. and Lewis, M.A. (1996) Dispersal, population growth, and the Allee effect: dynamics of the house finch invasion of eastern North America, *Am. Nat.* 148, 255–274

33 Knowlton, N. (1992) Thresholds and multiple stable states in coral reef community dynamics, *Am. Zool.* 32, 674–682

34 Wake, D.B. (1991) Declining amphibian populations, *Science* 253, 860

35 Allee, W.C. (1931) *Animal Aggregations, a Study in General Sociology*, University of Chicago Press

36 Aviles, L. and Tufino, P. (1998) Colony size and individual fitness in the social spider *Anelosimus eximius*, *Am. Nat.* 152, 403–418

37 Mistri, M. and Ceccherelli, V.U. (1996) Effects of a mucilage event on the Mediterranean gorgonian *Paramuricea clavata*. 1: short term impacts at the population and colony levels, *It. J. Zool.* 63, 221–230

38 Jarvis, J.U.M., Bennett, N.C. and Spinks, A.C. (1998) Food availability and foraging by wild colonies of Damaraland mole-rats (*Cryptomys damarensis*): implications for sociality, *Oecologia* 113, 290–298

39 Ghazoul, J., Liston, K.A. and Boyle, T.J.B. (1998) Disturbance-induced density dependent seed set in *Shorea siamensis* (Dipterocarpaceae), a tropical forest tree, *J. Ecol.* 86, 462–473

40 Brown, C.R., Stuchbury, B.J. and Walsh, P.D. (1990) Choice of colony size in birds, *Trends Ecol. Evol.* 5, 398–403

41 Roll, J. *et al.* (1997) Reproductive success increases with local density of conspecifics in a desert mustard (*Lesquerella fendleri*), *Conserv. Biol.* 11, 738–746

42 Groom, M.J. (1998) Allee effects limit population viability of an annual plant, *Am. Nat.* 151, 487–496

43 Noon, B.R. and McKelvey, K.S. (1996) Management of the spotted owl: A case history in conservation biology, *Annu. Rev. Ecol. Syst.* 27, 135–162

44 Hopper, K.R. and Roush, R.T. (1993) Mate finding, dispersal, number released, and the success of biological-control introductions, *Ecol. Entomol.* 18, 321–331

45 Green, R.E. (1997) The influence of numbers released on the outcome of attempts to introduce exotic bird species to New Zealand, *J. Anim. Ecol.* 66, 25–35

46 Woodroffe, R. *et al.* (1997) *The African Wild Dog. Status Survey & Conservation Action Plan*, IUCN

47 Fanshawe, J.H. and Fitzgibbon, C.D. (1993) Factors influencing the hunting success of an african wild dog pack, *Anim. Behav.* 45, 479–490

48 Gorman, M.L. *et al.* (1998) High hunting costs make African wild dogs vulnerable to kleptoparasitism by hyaenas, *Nature* 391, 479–480

49 Malcom, J.R. and Marten, K. (1982) Natural selection and the communal rearing of pups in African wild dogs (*Lycaon pictus*), *Behav. Ecol. Sociobiol.* 10, 1–13

50 Krafsur, E.S. (1998) Sterile insect technique for suppressing and eradicating insect population: 55 years and counting, *J. Agr. Entomol.* 15, 303–317

51 McCallum, H. (1996) Immunocontraception for wildlife population-control, *Trends Ecol. Evol.* 11, 491–493

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