

Decoupling of component and ensemble density feedbacks in birds and mammals

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Abstract. A component density feedback represents the effect of change in population size on single demographic rates, whereas an ensemble density feedback captures that effect on the overall growth rate of a population. Given that a population's growth rate is a synthesis of the interplay of all demographic rates operating in a population, we test the hypothesis that the strength of ensemble density feedback must augment with increasing strength of component density feedback, using long-term censuses of population size, fertility, and survival rates of 109 bird and mammal populations (97 species). We found that compensatory and depensatory component feedbacks were common (each detected in ~50% of the demographic rates). However, component feedback strength only explained <10% of the variation in ensemble feedback strength. To explain why, we illustrate the different sources of decoupling between component and ensemble feedbacks. We argue that the management of anthropogenic impacts on populations using component feedbacks alone is ill-advised, just as managing on the basis of ensemble feedbacks without a mechanistic understanding of the contributions made by its components and environmental variability can lead to suboptimal decisions.

Key words: *compensation; conservation; density dependence; depensation; fertility; management; mortality; population regulation; recruitment; survival.*

INTRODUCTION

Quantifying variation in population size is an important element for predicting population dynamics. In models where a demographic rate responds to change in population size, such density-dependent relationships are ecologically understood as demographic signals of trophic and social interactions (Herrando-Pérez et al. 2012), because the intensity of those interactions varies with population size. As the populations of long-lived species refill their environments following disturbance, the mechanisms associated with compensatory density feedback can sequentially reduce survival of juveniles, delay age of primiparity, depress fertility, and reduce adult survival, and this cascade of events can shape population trajectories (Eberhardt 2002). In fact, compensatory density feedback describes the theoretical capacity of populations to adjust growth and rebound from low, or decline from high, numbers (Fowler 1981, Eberhardt et al. 2008) as per capita availability of resources and exposure to processes such as competition, migration, predation and/or parasitism shift. As a determinant of a population's growth rate, density dependence is thus a key metric in the management of human influences on populations (Henle et al. 2004),

often modeled in combination with weather and climatic conditions (e.g., Coulson et al. 2001, Post et al. 2009).

Population growth models, which encompass the family of models of self-limiting growth (e.g., logistic equations), have become a popular tool in describing and predicting trajectories of population growth in time series of abundance (Eberhardt et al. 2008). Whenever ecological research focuses on assessing long-term population trends, those models are pragmatically cost-effective because a census of abundance alone can capture the net effects of population size on the instantaneous growth rate, r (i.e., proportional change in population size between two time steps such as years or generations): the mechanistic underpinning being that r encapsulates the compound interplay (ensemble) of all component fertility and survival rates (Münster-Swendsen and Berryman 2005). There is considerable empirical and theoretical support for such an assumption in homeotherms; thus, r has been decomposed into the contributions of age-structured fertility and survival rates (Coulson et al. 2005). Further, the largest sensitivities to population growth rate can shift from survival to fertility across species from slow to fast life histories (Oli and Dobson 2003), and both fertility and survival can track population trends in some mammals (Owen-Smith et al. 2005) and birds (Paradis et al. 2002). It can therefore be expected that the deterministic (i.e., via density feedback from trophic and social interactions) and stochastic (e.g., from system shocks such as storms, fires, floods) variation in demographic rates

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should leave a signal in time series of abundance. For instance, density feedback on adult survival (particularly females) exerts strong effects on growth rates of long-lived vertebrates, and those effects are measurable through population growth curves (Eberhardt 2002, Owen-Smith 2006). Understanding such signals has important implications; Kolb et al. (2010) illustrated that population growth rates can be insensitive to density feedback on some demographic rates (e.g., seed production). Consequently, limited resources and conservation measures can be wasted, and population trends can be inferred mistakenly, particularly because populations might be "... able to buffer the detrimental effects of small population size on vital rates that have a relatively small influence on population growth rate" (Kolb et al. 2010). Here we test the hypothesis that the strength of density feedback on r correlates positively with the strength of density feedback on single demographic rates in a data set consisting of long-term, annual estimates of population size and demographic rates for 97 species of birds and mammals. We conclude that even though stage-structured demographic rates are essential to elucidate important demographic mechanisms, long-term monitoring of population size as the basis of population growth models remains an irreplaceable component in ecological, management, and conservation research.

METHODS

We selected bird and mammal studies in *Science Citation Index* focusing on annual time series of both abundance and demographic rates from single populations. Subsequently, we gathered data sets from authors by e-mail, and from the selected publications when the data were provided. The final collection of data sets contained 294 time series of demographic rates (182 for fertility, 112 for survival) from 109 populations (74 birds, 35 mammals) and 97 species (65 birds, 32 mammals; see Plate 1). We give data sources in the Supplement. Fertility rates predominated in birds (80%), and survival rates did so in mammals (61%). Each population was represented by one time series of population size, and 1–11 demographic rates (median = 2 rates/population with a 95% range of 1–6; by 95% range, we mean that 95% of the ordered observations are above the reported low percentile and below the reported high percentile [low percentile, high percentile]). Fertility (e.g., clutch size, number of daughters per female) and mortality (proportion of dead bodies to total density) rates were single annual estimates, and survival (e.g., survival probability) and recruitment (e.g., percent surviving between two age classes) rates were relative estimates from one year to the next (we provide a concise description of all demographic rates in the Supplement). As opposed to fecundity (physiological maximum reproductive potential), all fertility rates were measures of current reproductive output (*sensu* Bradshaw and McMahon 2008). Time-series length varied

between 8 and 56 years (median of 18 years; 95% range of 9–45). We obtained species' body sizes (length from tip of nose/beak to tip of tail) through experts and online sources; body lengths ranged from 100 to 200 mm (e.g., Pied Flycatcher, *Ficedula hypoleuca* or short-tailed shrew, *Blarina brevicauda*) to >1 m (e.g., mute swan *Cygnus olor* or moose *Alces alces*), and had an approximately Gaussian distribution on a log-scale, indicating no bias toward either end of the spectrum of body sizes. We stored and analyzed all data in R 2.1 (R Development Core Team 2010).

Given the historical confusion in the lexicon of density dependence (Berryman et al. 2002, Herrando-Pérez et al. 2012), a terminological note is mandatory here. In this study, we refer to density dependence and density feedback interchangeably. We partially follow the unambiguous terms by Stephens et al. (1999), whereby density operating on single demographic rates (individual fitness) represents component feedback, and density operating on r (total fitness) represents ensemble (Stephens et al. [1999] refer to this as "demographic") feedback. As to component feedbacks, they can be compensatory when fertility and survival rates decrease with increasing population size (direct density dependence; Allee 1941), and depensatory when those rates decrease with declining numbers (inverse density dependence; Allee 1941). We assessed depensatory feedbacks across the measured range of population sizes, so make no claim for the evidence of Allee effects (i.e., depensation only at low numbers). Because different density feedbacks can operate in the same population both between consecutive, and delayed beyond two, time steps (Brook and Bradshaw 2006), and immediate and delayed density dependence are associated with different ecological mechanisms (Turchin 1990), we focused our analyses only on density feedbacks measurable between consecutive years.

We estimated ensemble feedback strength as the slope of the relationship of r [$= \log_e(N_{t+1}/N_t)$] vs. population size on a log scale, namely the Gompertz-logistic model (Medawar 1940, Nelder 1961) represented as

$$\log_e\left(\frac{N_{t+1}}{N_t}\right) = a + b \log_e(N_t) + \varepsilon_t \quad (1)$$

where N_t = population size at time t , a = intercept, b = strength of ensemble density feedback, and ε_t = Gaussian random variable with a mean of zero and a variance σ^2 reflecting uncorrelated stochastic variability in r . Because the Gompertz-logistic model is measured on a proportional scale, it characterizes the multiplicative nature of demographic rates better than the Ricker-logistic model, and clearly informs the strength of density dependence (Doncaster 2008). Furthermore, the Gompertz-logistic model has performed robustly in describing the general dynamics of populations of birds and mammals over a wide range of body sizes (e.g., Saitoh et al. 1997, 1999, 2008, Wang et al. 2002, 2009, White et al. 2007, Seavy et al. 2009, Pasinelli et al. 2011),

is present in multi-model inference scenarios where competing models are contrasted (Saitoh et al. 1997, Zeng et al. 1998, Fryxell et al. 2005, Chamaillé-Jammes et al. 2008, McMahon et al. 2009), is the top-ranked model in meta-analyses of hundreds of species in which various alternatives have also been evaluated (e.g., Brook and Bradshaw 2006), and has been a model used in theoretical development about density feedback (e.g., Dennis et al. 2006). We avoided fitting the fully parameterized θ -logistic model, due to recent caveats of application to analyses of time series (Clark et al. 2010), or other highly parameterized analogues (e.g., hyperbolic growth). Most species were from temperate and polar regions, the demographic rates of which are subject to strong annual seasonality, so we deemed year-round demographic estimates appropriate measures of population turnover.

We estimated component feedback strength as the slope of the relationship of each demographic rate and population size on a log scale (e.g., Paradis et al. 2002). Prior to model fitting, we expressed all demographic rates in standard deviation units by z -score standardization; for proportions p (most survival and recruitment rates), the standard deviation was calculated as $\sqrt{\bar{p}} \times [1 - \sqrt{\bar{p}}]/q$, where q is the number of observations in each time series and \bar{p} is the mean proportion. In quantifying component feedbacks, we used a Gaussian probability density function for all demographic rates, after checking normality of residuals in Q-Q and residual plots. For each population, we contrasted statistical evidence for both ensemble and component density feedbacks against an intercept-only model by means of Akaike's information criterion adjusted for finite sample size, AIC_c (Burnham and Anderson 2002).

We counted the number of demographic rates showing compensatory and depensatory component feedbacks for populations with and without AIC_c support for compensatory ensemble feedback (i.e., Gompertz-logistic growth). For those populations bearing evidence for Gompertz-logistic growth, the strength of compensatory ensemble feedback (response) was correlated with the strength of component feedback (only compensatory, only depensatory, and both pooled) through linear modeling in a model set including (1) an intercept-only model; (2) a model including the length of the time series (q), since q can correlate with the weight of evidence for ensemble feedback (Brook and Bradshaw 2006); (3) a model including both q and body size, to account for the decreasing intrinsic growth rate and increasing generation times from small- to large-bodied species (Peters 1983); and (4) a full model including q , body size, and strength of component feedback. We applied the same model contrast to subsets of time series of abundance and demographic rates showing different evidence ratios (ER) for ensemble and component feedbacks. ER for ensemble feedback (ER_{EN}) was (Gompertz-logistic growth $wAIC_c$)/(intercept-only model $wAIC_c$), and ER for component

feedback (ER_{CF}) was (linear model $wAIC_c$)/(intercept-only model $wAIC_c$) (Burnham and Anderson 2002).

Prior to model fitting, we converted the strengths of component and ensemble feedbacks to their absolute values; generally, raw values of feedback strength are negative or positive when compensatory or depensatory, respectively. We rescaled all explanatory variables by their logarithms to approximate a linear relationship with the response. Furthermore, to meet assumptions for the saturated model, we used a Gaussian variance function and expressed the response on a proportional scale through a square-root transformation, as supported by a likelihood-based test of Box and Cox (1964) for all data subsets.

RESULTS

Ensemble density feedback

Of the total of 109 time series of population size used in our study, we found information-theoretic support (i.e., evidence ratio (ER_{EN}) > 1) for compensatory ensemble density feedback (i.e., Gompertz-logistic growth) in 71% of the populations, 51 of 74 birds (69%) and 26 of 35 mammals (74%). Five populations of large-bodied species showed depensatory ensemble density feedback: these were steadily recovering from low abundances (Bearded Vulture, *Gypaetus barbatus* and African elephant, *Loxodonta loxodonta*), or steadily declining (tsessebe, *Damaliscus lunatus* and sable antelope, *Hippotragus niger* and roan antelope, *Hippotragus equinus*); we removed those time series from the statistical descriptors hereafter. The median ER_{EN} was 3.3 (95% range, 0.2 to >1000), so overall the density-feedback model was just over three times more likely than the density-independent model, given the data. ER_{EN} was relatively skewed (Fig. 1); this prompted us to investigate ensemble feedbacks (and component feedbacks, see *Component density feedback*) over different ER_{EN} magnitudes.

The median strength of compensatory ensemble feedback across the subset of populations with ER_{EN} > 1 was -0.4 (-1.3 to -0.1); thus, an average increase in population size by one order of magnitude resulted in a ~ 0.5 -fold decrease ($e^{0.4} - 1$) in population growth rate. For ER_{EN} > 2, 4, 8, 16, and 32, median strength of ensemble feedbacks ranged from -0.6 to -0.5 . We measured the strongest ensemble feedbacks for the Seychelles Warbler, *Acrocephalus sechellensis* (-1.5) and the Tawny Owl, *Strix aluco* (-1.3) in birds, and the short-tailed shrew, *Blarina brevicauda* (-1.5) and the pygmy possum, *Thylamys elegans* (-1.2) in mammals. ER_{EN} and median strengths of ensemble feedback were of the same magnitude in birds and mammals (Appendix A: Fig. A1).

Component density feedback

We found statistical evidence for component density feedback (i.e., evidence ratio ER_{CF} > 1) in all 294 time series of demographic rates. Furthermore, ER_{CF} were

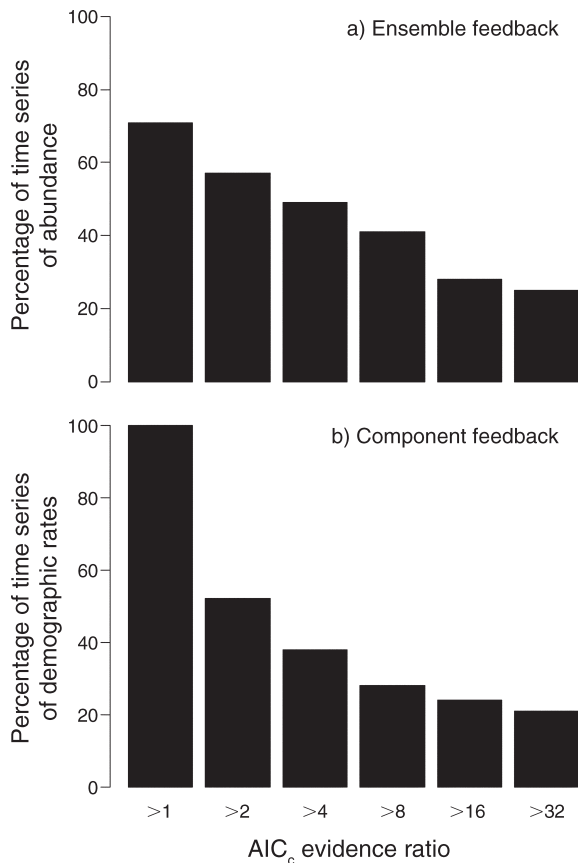


FIG. 1. Proportion of time series of abundance ($n = 109$ populations) and demographic rates ($n = 294$) showing different strengths of Akaike's information criterion adjusted for finite sample size (AIC_c) evidence for ensemble and component feedbacks for 97 species of mammals and birds.

more skewed than ER_{EN} (Fig. 1), with the median $ER_{CF} = 2.1$ (1.0 to >1000). About 50% of the component feedbacks were compensatory, and the other half were depensatory (but not necessarily showing Allee effects; see *Methods*). We found that (1) both compensatory and depensatory component feedbacks occurred whether or not there was statistical support for ensemble density feedback (Tables 1 and 2), (2) compensatory feedbacks

on survival and fertility dominated when ensemble feedback was present (Tables 1 and 2), and (3) the predominance of compensatory feedback occurred mainly in survival for those populations showing the highest ER_{EN} (>4 ; Appendix B: Tables B1 and B2). That pattern was consistent for other ER_{EN} thresholds higher than 4.

The median strength of compensatory feedback was -1.3 (-5.6 to -0.1) for survival and -0.7 (-5.2 to 0.0) for fertility. In other words, increases in population size by one order of magnitude resulted in ~ 2.6 -fold decrease in survival ($e^{1.3} - 1$) and ~ 1.0 -fold decrease in fertility ($e^{0.7} - 1$), measured in standard deviation units (see *Methods*). For depensatory feedback, strength ranged between 0.6 (0.1 to 3.2) (survival) and 0.7 (0.1 to 2.8) (fertility). The strongest component feedbacks by main taxa occurred in the southern elephant seal, *Mirounga leonina* (-11.1 , births per adult) and Common Guillemot, *Uria aalge* (-3.9 , chicks per breeding pair; compensatory), and giraffe, *Giraffa camelopardalis* (12.8, juveniles per female) and Eastern Kingbird, *Tyrannus tyrannus* (3.0, proportion of breeding returnees; depensatory). Median strengths were relatively larger in compensatory than in depensatory component feedbacks only for survival rates (Tables 1 and 2), across different ER_{EN} and ER_{CF} magnitudes (Tables 1 and 2; Appendix B: Tables B1 and B2). Median ER_{CF} and strength of component feedback were of the same magnitude in mammals and birds (results not shown).

Relationship between ensemble and component feedback strength

We found weak correlation between the strength of ensemble and component feedbacks, after controlling for the length of the time series, and body size (Table 3, Fig. 2). The AIC_c top-ranked component feedback models explained between 5% and 33% of variation (deviance) in ensemble feedback strength across populations. Component feedback strength occurred in a top-ranked model when all survival rates were analyzed separately (3.8% variation in ensemble feedback strength explained), and for survival (9.9% variation explained), and fertility (4.1% variation explained) rates experiencing compensatory component feedback (Table 3). The

TABLE 1. Frequency (%) of occurrence of compensatory and depensatory component density feedbacks on survival rates in bird and mammal populations supported ($ER_{EN} > 1$) or not ($ER_{EN} < 1$) for ensemble density feedback (i.e., Gompertz-logistic growth).

Component feedback type	Ensemble-feedback support (ER_{EN})	Component feedback frequency (%)		Component feedback strength	
		$ER_{CF} > 1$	$ER_{CF} > 4$	$ER_{CF} > 1$	$ER_{CF} > 4$
Compensatory	>1	55	61	-1.2 (-5.7 to -0.1)	-1.8 (-7.7 to -0.5)
	<1	6	8	-2.4 (-3.2 to -0.2)	-3.2 (-3.2 to -1.9)
Depensatory	>1	25	18	0.6 (0.1 to 3.0)	0.9 (0.5 to 3.2)
	<1	14	15	0.6 (0.2 to 4.6)	2.2 (1.1 to 5.2)

Notes: Frequencies are given for survival rates showing evidence (evidence ratio, $ER_{CF} > 1$, $n = 106$ rates) or strong evidence ($ER_{CF} > 4$, $n = 56$ rates) for component feedback (CF), split by whether or not populations show ensemble density feedback (ER_{EN}). Median strengths of component density feedback with 95% percentile ranges (in parentheses) are also reported.

TABLE 2. Frequency (%) of occurrence of compensatory and depensatory component density feedbacks on fertility rates in bird and mammal populations supported ($ER_{EN} > 1$) or not ($ER_{EN} < 1$) for ensemble density feedback (i.e., Gompertz-logistic growth).

Component feedback type	Ensemble-feedback support (ER_{EN})	Component feedback frequency (%)		Component feedback strength	
		$ER_{CF} > 1$	$ER_{CF} > 4$	$ER_{CF} > 1$	$ER_{CF} > 4$
Compensatory	>1	36	44	-0.7 (-5.4 to -0.0)	-1.8 (-6.9 to -0.4)
	<1	15	11	-0.8 (-3.6 to -0.0)	-1.8 (-3.8 to -0.5)
Depensatory	>1	27	29	0.8 (0.1 to 2.8)	1.1 (0.6 to 8.1)
	<1	22	16	0.6 (0.1 to 2.5)	2.0 (0.5 to 4.4)

Notes: Frequencies are given for fertility rates showing evidence (evidence ratio, $ER_{CF} > 1$, $n = 176$ rates) or strong evidence ($ER_{CF} > 4$, $n = 70$ rates) of component feedback, split by whether or not populations show ensemble density feedback (ER_{EN}). Median strengths of component density feedback with 95% percentile ranges (in parentheses) are also reported.

length of time series (0.5–6.1%) and body size (2.7–28.1%) accounted for most of the variation explained in ensemble feedback strength in the top-ranked models. When using subsets of demographic rates from populations scoring $ER_{EN} > 4$ and $ER_{CF} > 1$ (Appendix C: Table C1), the best correlation between component and ensemble feedbacks occurred for compensatory survival rates (9.9% of the variation explained). The effects of component on ensemble feedback strength were not detectable statistically for times series with $ER_{EN} > 4$ and $ER_{CF} > 4$ (Table C2), and when mammals and birds were analyzed separately across all ER magnitudes, although sample sizes in all of the former data subsets were small (results not shown).

DISCUSSION

We have identified a serious decoupling in the strength, direction, and occurrence of density feedbacks operating on single demographic rates and population growth rates of birds and mammals. With regard to strength, the intensity with which density feedback alters individual demographic rates does not necessarily translate into a similar intensity of feedback on a population’s rate of growth (indeed, this seems rare). As

to feedback direction, many populations can arrest their growth rate even though some fertility and survival rates are being enhanced (depensating) at high numbers. As for feedback occurrence, depensating and compensating demographic rates occurred in a number of populations showing no compensatory response to population increase. Since a population grows when births and immigration outnumber deaths and emigration, the decoupling of ensemble and component feedbacks must originate from a failure in (1) measuring density feedback on the survival and fertility rates most affected by demographic processes, (2) accounting for dispersal (i.e., populations are not closed), or (3) incorporating external forces, such as climate, that can shape demographic rates and relax or remove the demographic effects of the social and trophic interactions eliciting density feedback. In the following, we illustrate those scenarios with selected case studies classified into the three main types of component ensemble decoupling (Table 4, Fig. 3). We were mainly interested in cases where decoupling existed, yet there were examples of strongly coupled component and ensemble feedbacks (in terms of strength, direction, and occurrence), such as in the Great Partridge, *Perdix perdix*, in the Plateau Aigre

TABLE 3. Ensemble feedback strength (EN) fitted as a function of sample size in the time series (q , years), body size (BL = body length, mm), and component feedback strength (CF) in birds and mammals.

Rates	N	Component feedback type	Top-ranked models	$wAIC_c$	DE_{total} (%)	DE_q (%)	DE_{BL} (%)	DE_{CF} (%)
All	195	all	$EN \sim q + BL$	0.70	7.5	3.3	7.2	
Fertility	112	all	$EN \sim q + BL$	0.60	8.4	4.3	4.1	
Survival	83	all	$EN \sim q + BL + CF$	0.66	16.4	1.3	11.3	3.8
All	122	compensatory	$EN \sim q + BL$	0.42	4.6	1.9	2.7	
Fertility	65	compensatory	$EN \sim q + BL + CF$	0.44	13.8	4.1	9.7	4.1
Survival	57	compensatory	$EN \sim q + BL + CF$	0.69	16.1	0.5	5.7	9.9
All	73	depensatory	$EN \sim q + BL$	0.58	13.8	6.1	7.7	
Fertility	47	depensatory	$EN \sim q$	0.34	5.4	5.4		
Survival	26	depensatory	$EN \sim q + BL$	0.69	33.2	5.1	28.1	

Notes: N is the number of demographic rates included in each model contrast, $wAIC_c$ is the model probability (only top-ranked models in a set are shown), and DE is the percentage of deviance explained (total and broken down by predictors). Model fits were done using all demographic rates, split by fertility or survival rates, and all types of component feedback, split whether they were compensatory or depensatory. All demographic rates from populations supported for ensemble feedback ($ER_{EN} > 1$, Tables 1 and 2) are included. The response variable, EN, is the strength of (Gompertz-logistic) ensemble density feedback (square root-transformed). Predictors are: q , number of annual time steps in the paired time series of abundance and demographic rates; BL, body length for each species from tip of nose/beak to end of tail; CF, strength of linear component feedback. All predictors were log-transformed. The model set is $EN \sim 1$; $EN \sim q$; $EN \sim q + BL$; $EN \sim q + BL + CF$. No deviance is calculated for predictors that are not in top-ranked models.

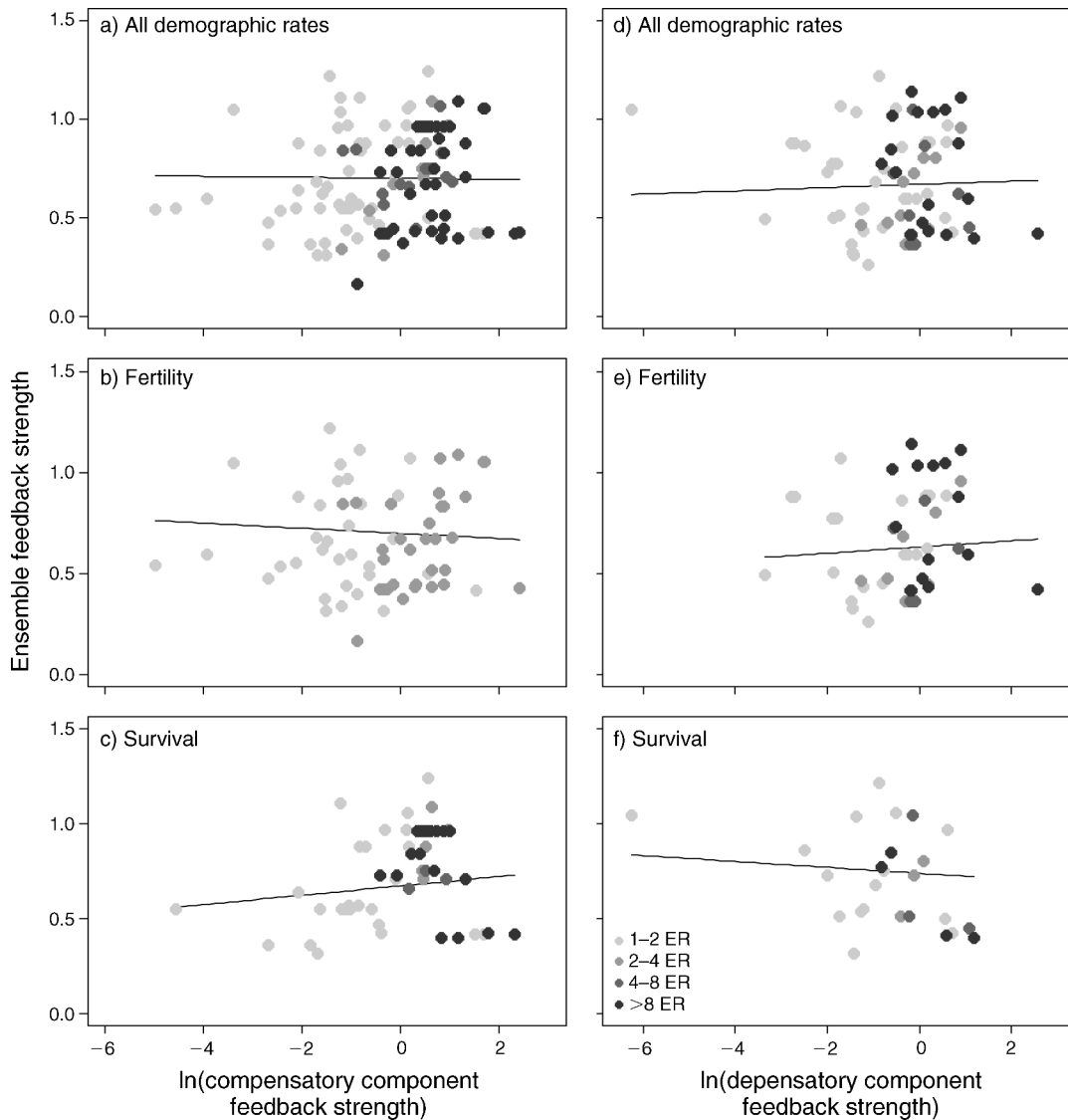


FIG. 2. Relationship between component (CF) and ensemble (EN) density feedback strength in populations of birds and mammals. For each population, ensemble feedback strength is the slope of Gompertz-logistic growth based on time series of abundance, and component feedback strength is the linear slope between each measured demographic rate and abundance. Left (a, b, c) and right (d, e, f) panels equate compensatory and depensatory component feedbacks, respectively. Shading of points distinguishes the magnitude of AIC_c-evidence ratios (ER) for component feedback (i.e., ER_{CF}). Linear trends are for the model $EN \sim q + BL + CF$ with q (log-transformed time series length, years) and BL (log-transformed body size, mm) held constant at their mean (see Table 3). All demographic rates from populations showing evidence for compensatory ensemble feedback (ER_{EN} > 1; Tables 1 and 2) are included.

(Bro et al. 2002), or the African elephant, *Loxodonta africana*, in Addo National Park, South Africa (Gough and Kerley 2006) (Table 4, Fig. 3).

Sources of decoupling

The first category of observed decoupling occurred in feedback direction when a compensatory ensemble feedback existed simultaneously with a depensatory component (Table 4, Fig. 3). An example was the short-tailed shrew, *Blarina brevicauda*, in the deciduous forest of the Appalachian Plateau, USA. The population

had experienced compensatory ensemble feedback for more than two decades. Along those lines, first-order ensemble feedback from competitive interactions has been suggested to govern the dynamics of this population (Merritt et al. 2001). Likewise, we found that recruitment (probability of an individual at time $t + 1$ being a new recruit from time t) was compensatory, yet survival rates were depensatory. We detected the same pattern in two other small mammals: the leaf-eared mouse *Phyllotis darwini* (Lima et al. 2001a) and the mouse opossum *Thylamys elegans* (Lima et al. 2001b)

TABLE 4. Coupled and decoupled relationships between component and ensemble density feedbacks on populations of birds and mammals. Types (a–g) refer to panels in Fig. 3.

Feedback and species	Site	Demographic rate	Years	Reference
a) Coupled: direction; EN, CF (both compensatory)				
Black-throated Blue Warbler (<i>Dendroica caerulescens</i>)	New Hampshire, USA	fledglings/territory, adult survival	1986–1999	Rodenhouse et al. (2003)
Great Partridge (<i>Perdix perdix</i>)	Plateau Aigre, France	chicks/female in summer	1989–2000	Bro et al. (2002)
Pigmy possum (<i>Burramys parvus</i>)	Snowy Mountain, Australia	daughters/female, female survival	1986–1997	McCarthy and Broome (2000)
Soay sheep (<i>Ovis aries</i>)	Kilda Archipelago, Scotland	adult and juvenile recruitment, adult and juvenile survival	1985–2007	Coulson et al. (2005)
b) Coupled: direction; EN, CF (both depensatory)				
African elephant (<i>Loxodonta africana</i>)	Addo National Park, South Africa	breeding/reproductive females, non-pregnant/pregnant females	1976–2002	Gough and Kerley (2006)
Sable antelope (<i>Hippotragus niger</i>)	Kruger National Park, South Africa	juveniles/female, yearling recruitment	1977–1996	Owen-Smith et al. (2005)
c) Decoupled: direction; EN (compensatory), CF (depensatory)				
Black-browed Albatross (<i>Diomedea melanophris</i>)	Bird Island, Southern Ocean	fledglings/clutch size	1976–1992	Prince et al. (1994)
Emperor Penguin (<i>Aptenodytes forsterii</i>)	Terre Adélie, Antarctica	chicks/breeding pair, fledglings/breeding pair	1962–2005	Jenouvrier et al. (2009)
Leaf-eared mouse (<i>Phyllotis darwini</i>)	Las Chinchillas Reserve, Chile	female survival	1997–2007	Lima et al. (2001a)
Short-tailed shrew (<i>Blarina brevicauda</i>)	Appalachian Plateau, USA	individual survival	1979–1999	Merritt et al. (2001)
d) Decoupled: direction; EN (depensatory), CF (compensatory)				
Bearded Vulture (<i>Gypaetus barbatus</i>)	Pyrenees, Spain	fledglings/breeding pair	1978–2002	Carrete et al. (2006)
Roan antelope (<i>Hippotragus equinus</i>)	Kruger National Park, South Africa	juveniles/female	1977–1996	Owen-Smith et al. (2005)
e) Decoupled: strength; EN stronger than CF (both compensatory)				
Island fox (<i>Urocyon littoralis</i>)	San Clemente Island, California, USA	adult survival	1988–1997	Angulo et al. (2007)
Tawny Owl (<i>Strix aluco</i>)	Lahti, Fennoscandia, Finland	fledglings/breeding pair	1981–1995	Karell et al. (2009)
f) Decoupled: strength; CF stronger than EN (both compensatory)				
Barnacle Goose (<i>Branta leucopsis</i>)	Laus Holmar Islands, Sweden	hatchlings/successful nest	1985–1993	Larsson and Forslund (1994)
Osprey (<i>Pandion haliaetus</i>)	Corsica, France	fledglings/breeding pair, fledglings/hatchlings	1974–2004	Bretagnolle et al. (2008)
Southern elephant seal (<i>Mirounga leonina</i>)	Marion Island, Indian Ocean	births/adult, proportion of dead pups	1986–1999	Pistorius et al. (2008)
g) Decoupled: occurrence; EN (no evidence), CF (compensatory)				
Barn Swallow (<i>Hirundo rustica</i>)	Kraghede, Denmark	first and second brood size, adult survival	1971–2009	Møller (1989)
Black-tailed deer (<i>Odocoileus columbianus</i>)	King Creek, Washington, USA	fawn recruitment	1979–1997	Gilbert and Raedeke (2004)
Eastern Kingbird (<i>Tyrannus tyrannus</i>)	Charlotte Valley, Delaware, USA	fledglings/breeding pair	1983–2005	Murphy (2001a)
Impala (<i>Aepyceros melampus</i>)	Kruger National Park, South Africa	adult survival	1982–1995	Owen-Smith et al. (2005)

Notes: Variables in the feedback descriptions are: EN, ensemble density feedback; CF, component density feedback.

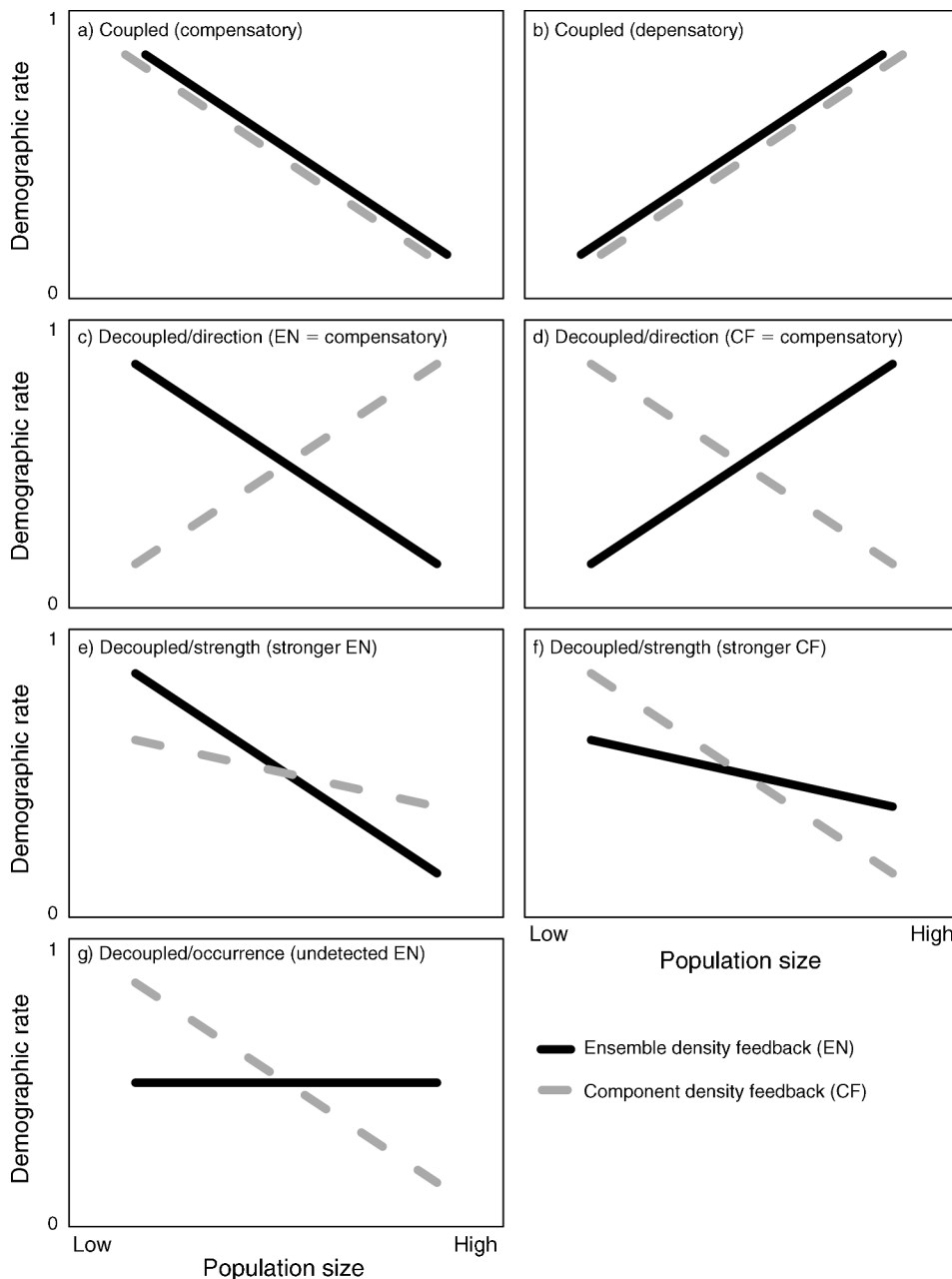


FIG. 3. Coupled and decoupled relationships between component and ensemble density feedbacks under examination. Panels represent demographic rates (ordinate; namely, fertility at time t , or population growth rate or survival from time $t - 1$ to t) plotted against population size (abscissa; census data) at time $t - 1$. Compensatory feedbacks imply decreasing population growth rates, survival, or fertility rates as population size increases (negative slope). Depensatory feedbacks imply increasing population growth, survival and fertility rates as population size increases (positive slope). Abbreviations are: EN, ensemble density feedback (i.e., on population growth rates; black continuous line); CF, component density feedback (i.e., on survival or fertility rates; gray dashed line). Panels (a)–(g) reference types of coupling/decoupling in Table 4.

from thorn scrub in Chile. In small rodents such as the leaf-eared mouse, compensatory population growth rates can buffer depensatory survival when losses of adult individuals are mainly caused by stable populations of generalist predators that do not respond numerically to prey abundance (Lima et al. 2001a), so the larger the mouse population, the higher the chances

of escaping predation (M. Lima, *personal communication*).

Conversely, shrinking ice cover lowered adult survival of Emperor Penguins, *Aptenodytes forsteri*, in Terre Adélie, Antarctica, over the last half century, resulting in a steady population decline (Jenouvrier et al. 2009). For a population largely affected by climate conditions, we

indeed found only moderate compensatory ensemble feedback, and moderate-to-weak compensatory component feedback on survival of adults and yearlings. However, the component feedback was relatively strong and depensatory on all fertility rates, including number of chicks per breeding pair, fledglings per clutch, and proportion of adult breeders and 5-year breeders over adult and 5-year adult population size. This species forms colonies far from open sea, so large ice cover forces individuals to make long foraging trips, compromising food supply to chicks and hatching success (Zimmer et al. 2008). Therefore, even if the population declines as the ice sheet reduces in extent, surviving adults might improve reproduction if the energetic costs of foraging diminish. Most importantly, those shifts in fertility could be attributed to climate modifying the penguin's habitat, thus not constituting genuine density feedbacks (i.e., triggered by social and/or trophic interactions in the population).

An extreme case for decoupling in feedback direction is the island fox, *Urocyon littoralis*, off California, USA. By amalgamating population estimates for six islands, Angulo et al. (2007) report depensatory component feedback on adult and pup survival (linked to predation by Golden Eagles, *Aquila chrysaetos*), and on proportion of breeding females. Yet, for the population on San Clemente Island we found strong compensatory ensemble feedback, with strong to moderate compensatory feedbacks on number of kits per female and adult survival, suggesting that survival and fertility rates are not enhanced (Angulo et al. 2007), but are instead depressed as population size increases.

The second category of observed decoupling occurred in feedback strength when a relatively weak compensatory ensemble feedback coincided with a relatively strong compensatory component feedback (i.e., the lower-right corner of Fig. 2 panels), or vice versa (i.e., upper-left corner of Fig. 2 panels; Table 4, Fig. 3). For instance, the population of elephant seals, *Mirounga leonina*, on Marion Island, southern Indian Ocean, has fallen by ~30% in the last three decades, as part of an overall decline of this pinniped in the Southern Hemisphere (McMahon et al. 2005). We found a moderate compensatory ensemble feedback, yet relatively strong compensatory feedbacks on the ratio of births to total population size, proportion of pup deaths, and probability of female survival. Our estimates for component feedback agree with published studies (Pistorius et al. 2008). By finding the component feedback on survival, Pistorius et al. (2008) claim regulation for this population. However, the weak strength of ensemble feedback suggests that depensatory component feedbacks on unmeasured demographic rates might be counteracting compensatory survival rates, and/or that the change in key demographic rates is actually free of density feedback. Thus, shifts in food availability from environmental fluctuation might drive

the dynamics of this and other populations of southern elephant seals (McMahon et al. 2005).

A different pattern unfolded for a population of the Tawny Owl, *Strix aluco*, in a mosaic of spruce-dominated forest and agricultural land in Lahti, Finland. This population follows vole prey cycles tightly, such that recruitment of first-time breeders builds up the predator's numerical response to prey peaks, but the survival of experienced breeders during low-prey periods has the largest contribution to population growth (Karell et al. 2009). Over two decades of available data, we found one of the strongest compensatory ensemble feedbacks in our data set for this raptor, and contrastingly negligible component feedback on adult survival or number of fledglings per breeding pair. Many first-year recruits in the study area are immigrants (P. Karell, *personal communication*); hence, the strong ensemble feedback most likely reflects the emigration of adults out of the study area when the population exceeds carrying capacity.

The third category of observed decoupling consisted of absence of compensatory ensemble feedback even though some demographic rates were compensating (Table 4, Fig. 3). Two final study cases illustrate this scenario. Eastern Kingbird, *Tyrannus tyrannus*, shows high breeding-site fidelity in North America following migration from South America (Murphy 2001a). In a population nesting in upland hawthorns (*Crataegus* spp.) at Charlotte Valley in Delaware County, USA, we found no support for compensatory ensemble feedback ($ER_{EN} < 1$), and relatively large support for component feedback ($ER_{CF} > 6$) with strong compensatory and depensatory components on the number of fledglings per breeding pair, and the proportion of adults returning and breeding, respectively. Thus, fertility decreased in years when the breeding population was relatively large, whereas the number of breeding returnees in a given year tended to be larger when breeding numbers from the previous year were relatively high. Although population growth rate is much more sensitive to change in adult survival than fertility (Murphy 2001a), and correlates well with the steady decline in this population in the 1990s (Murphy 2001b), additional simulation work revealed that density feedbacks on survival or fertility are not driving population trends (Murphy 2001b), in consonance with our results. The population of this flycatcher functions as a sink, with adult survival heavily governed by habitat quality (Murphy 2001a, b).

Another illustrative example is the impala *Aepyceros melampus*, which is the most abundant ungulate of small to medium body size and the main prey of the largest savanna predators in Kruger National Park, South Africa. Using data spanning more than a decade, we found no support for ensemble feedback ($ER_{EN} < 1$), and relatively strong component feedbacks, which were compensatory on adult survival ($ER_{CF} > 4$), and depensatory on yearling survival ($ER_{CF} > 1000$), and



PLATE 1. Individuals from a sample of study populations/species for which we estimated component and ensemble density feedbacks (left to right, top to bottom): degu *Octodon degus*, semi-arid thorn scrub, Bosque Fray Jorge National Park, Chile (photo credit: Hector Veas Cortes); Black-throated Blue Warbler *Setophaga caerulescens*, mature hardwood forest, Washington D.C., USA (photo credit: Gerhard Hoffmann); Weddell seal *Leptonychotes weddellii*, Erebus Bay, Ross Sea, Antarctica (photo credit: Jay Rotella); Tawny Owl, mixed boreal forest, Lohja, Uusimaa, Finland (photo credit: Lasse J. Laine); Great Flamingo *Phoenicopterus roseus*, Fangassier Lagoon, Camargue, France (photo credit: Hellio van Ingen); reindeer *Rangifer tarandus*, Arctic tundra, Nordenskiöld Land, Svalbard, Norway (photo credit: Olav Strand/NINA); Emperor Penguin *Aptenodytes forsteri*, Terre Adélie, Antarctica (photo credit: Stephanie Jenouvrier).

number of juveniles per female ($ER_{CF} > 200$). The direction of component feedbacks coincides with comparable published estimates (Owen-Smith et al. 2005). Owen-Smith and Mills (2006) assert that factors driving the dynamics of this stable population remain poorly explained, showing that density (lagged or not) explains the least amount of variation in this population relative to ten other ungulate species at Kruger.

The extent of the decoupling between component and ensemble feedbacks observed across populations (Fig. 2) can also be partially accounted for by trade-offs among component feedbacks in populations where multiple vital rates have been measured. For instance, both Great Tits (*Parus major*) from the Pilis Mountains, Hungary, and bison (*Bison bison*) from Wood Buffalo National Park, Canada, showed strong evidence for compensatory ensemble feedback. In the Great Tits, the strongest compensatory component feedback involved clutch size, thus the observed milder or null compensatory effects of adult density on brood size and fledgling rates could originate from competition between Great Tits and Blue Tits (*P. caeruleus*) only at the time around egg laying (see Sasvári et al. 1987). In contrast, the bison population's strength of compensatory component feedback decreased through number of calves, one- and

two-year-old individuals per female, a pattern that could be related to specific age-class responses to predation, disease, and dispersal (see Bradley and Wilmshurst 2005). Where data exist only for single fertility or survival rates, those trade-offs therefore indicate strongly that population-based conclusions regarding density dependence can vary substantially according to what demographic rates researchers choose or are able to measure. We had access to only few demographic rates across sequential ages within the same population, so we could not assess this aspect further.

The disparity of types of demographic rates, and the variety of age/stage classes on which they were measured, might be a source of noise in our models. It would be interesting to explore whether the correlation between component and ensemble feedbacks improves by using a consistent set of demographic rates for all populations (e.g., Paradis et al. 2002), even for one or several well-represented age classes. If the data are available for a large number of populations involving several co-occurring demographic rates, trade-offs among component feedbacks could be fully examined across species. Furthermore, r encapsulates the totality of demographic processes acting on survival and reproduction (Münster-Swendsen and Berryman 2005), yet excludes dispersal

effects. However, measured changes in r can partly result from emigration and immigration, and magnify the decoupling between feedback on r and feedback on survival or fertility rates. Future research could circumvent this by controlling for known dispersal across populations, or selecting populations that are closed or monitored on spatial scales large enough to render dispersal effects negligible. Our analyses could be further expanded by looking at lags of density feedback on r and single demographic rates, and by exploring nonlinear feedbacks that the Gompertz-logistic model might capture poorly. Finally, population growth rate is bound to be shaped by the combined effect of many mechanisms. These can encompass density feedback (e.g., competition, parasitism, predation), environmental stressors (i.e., climate), food availability (e.g., vegetation, prey, and rapid evolution [such as change in beak size]). To account for these, and should available data permit their robust parameterization, models can be made arbitrarily complex to capture the dynamical nuisances of any given (meta)population. However, the exploration of macroecological patterns across populations and species relies on models comparable over entire life-history gradients, especially considering the extreme variation in the amount and type of demographic data available in even the best-studied taxa. We advocate that if broad-scale, year-round environmental data can be collated, our analyses could be improved by modeling demographic data along with environmental proxies as predictors in autoregressive models, or to represent variable carrying capacity in logistic models.

Conclusions

When the purpose is to ascertain the importance of density feedback on a population's growth rate, we see several important caveats in monitoring and/or making ecological inferences only from demographic rates. (1) Spurious compensatory feedbacks on overall demographic rates might occur simply because of the effects that population size can have on age structure (Festa-Bianchet et al. 2003), and how density-dependent and density-independent effects are partitioned across age-structured demographic rates. Likewise, trade-offs among the various demographic rates can be expected to result in feedback operating in some age classes and not others (e.g., Møller 1989). (2) Different component feedbacks might have synergistic effects on population growth rates; this seems to be the case for pest, exploited, or endangered populations subject to Allee effects, for which extinction thresholds might be highly uncertain if estimated only from single vital rates (Berec et al. 2007). (3) Some individuals might not experience the effects of regional population density, so component feedbacks pooled over several demographically isolated populations (e.g., Angulo et al. 2007) can confuse the direction and strength of the feedbacks experienced by single populations. (4) Whereas r will capture losses and gains due to emigration (as if they were survival or reproduction), studies assessing popula-

tion trends from only survival and/or fertility rates will fail to detect dispersal effects, and again miss crucial trade-offs among different component feedbacks. (5) Statistical relationships between population size and demographic rates can indicate environmental forcing free of density feedback over most of the measured range of population density (e.g., Gough and Kerley 2006, Jenouvrier et al. 2009), and operate in unison with genuine density feedbacks, as revealed for some populations (e.g., Rodenhuse et al. 2003). (6) In most situations, it will be logistically impossible to measure all survival, fertility and dispersal rates in a population. Furthermore, the methods to quantify them can vary considerably depending on the type of data collected, and the selection of biologically meaningful demographic rates will always require an extensive, often unavailable knowledge of the study population. Indeed, we collected data on >20 different types of demographic rates in up to 10 different age/stage classes, separating or not sexes, out of 109 independent studies. The choice of what to measure is unclear and subject to debate. (7) Most importantly, population regulation emerges solely as a net effect, namely when the effect of all compensatory component feedbacks overrides that of all compensatory component feedbacks (Sinclair and Pech 1996). In the absence of estimates of all demographic rates, regulation is defined by population parameters capturing long-term persistence, the tendency to return to equilibrium, and bounded fluctuations above extinction (Hixon et al. 2002). Therefore, conservation and management investment can be mistaken if occurrence or lack of regulation is inferred only from demographic rates, a common inference in our literature survey (e.g., Pöysä and Pesonen 2003, Gough and Kerley 2006, Pistorius et al. 2008). A striking consequence of such inference is that the occurrence of population regulation in wild populations might have been substantially overstated in the ecological literature.

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SUPPLEMENTAL MATERIAL

Appendix A

Evidence ratios and strength of ensemble density feedback comparing mammals and birds (*Ecological Archives* E093-150-A1).

Appendix B

Frequency of component density feedbacks according to different statistical support for component and ensemble feedback (*Ecological Archives* E093-150-A2).

Appendix C

Model metrics correlating strength of component and ensemble density feedbacks across magnitudes of statistical support for ensemble (ER_{EN}) and component (ER_{CF}) feedback (*Ecological Archives* E093-150-A3).

Supplement

Summary of populations and demographic rates included in this study (*Ecological Archives* E093-150-S1).