Restricted dispersal reduces the strength of spatial density dependence in a tropical bird population

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Spatial processes could play an important role in density-dependent population regulation because the disproportionate use of poor quality habitats as population size increases is widespread in animal populations—the so-called buffer effect. While the buffer effect patterns and their demographic consequences have been described in a number of wild populations, much less is known about how dispersal affects distribution patterns and ultimately density dependence. Here, we investigated the role of dispersal in spatial density dependence using an extraordinarily detailed dataset from a reintroduced Mauritius kestrel (*Falco punctatus*) population with a territorial (despotic) breeding system. We show that recruitment rates varied significantly between territories, and that territory occupancy was related to its recruitment rate, both of which are consistent with the buffer effect theory. However, we also show that restricted dispersal affects the patterns of territory occupancy with the territories close to release sites being occupied sooner and for longer as the population has grown than the territories further away. As a result of these dispersal patterns, the strength of spatial density dependence is significantly reduced. We conclude that restricted dispersal can modify spatial density dependence in the wild, which has implications for the way population dynamics are likely to be impacted by environmental change.

Keywords: buffer effect; recruitment; dispersal; spatial density dependence; reintroduction; Mauritius kestrel (*Falco punctatus*)

1. INTRODUCTION

A recurrent challenge to modern ecology is to be able to understand how populations are likely to respond to environmental change. Density dependence plays a crucial role in the dynamics of animal populations and in the way populations respond to environmental change (Brook *et al.* 1997; Pascual *et al.* 1997; Karels & Boonstra 2000; Fagan *et al.* 2001; Runge & Johnson 2002; Stewart *et al.* 2005; Viljugrein *et al.* 2005). While data have steadily accumulated on the patterns of density dependence in a wide range of species over the last 40 years (Sibly *et al.* 2005), our understanding of the underlying processes remains limited. Furthermore, for species of conservation concern, there is often a paucity of information on density-dependent patterns and mechanisms with which to aid management and reintroduction programmes. As a result, the models of population dynamics used to investigate population persistence in the face of environmental change often lack density dependence, or make strong assumptions about the underlying mechanism (Henle *et al.* 2004). It is important, therefore, to improve our understanding of density-dependent mechanisms in wild populations.

One potentially general mechanism of density dependence is the so-called ‘buffer effect’ in which an increasing proportion of individuals are forced by

pre-emptive use of high-quality habitat to occupy poorer quality habitat as a population grows, thereby driving down *per capita* vital rates and population growth (Brown 1969; Fretwell & Lucas 1970; Rodenhouse *et al.* 1997; McPeck *et al.* 2001). Spatial distribution patterns consistent with this idea are widespread in vertebrate populations (Sutherland *et al.* 2002), but our understanding of the links between spatial distribution patterns and demography is limited to a few ‘model’ systems (Ferrer & Donazar 1996; Holmes *et al.* 1996; Fernandez *et al.* 1998; Gill *et al.* 2001; Kruger & Lindstrom 2001; Rodenhouse *et al.* 2003; Sergio & Newton 2003; Kokko *et al.* 2004; Armstrong *et al.* 2005; Gunnarsson *et al.* 2005; Carrete *et al.* 2006; Soutullo *et al.* 2006; Sergio *et al.* 2007). Furthermore, little is known about how individual dispersal decisions shape distribution patterns and their consequences even in these well-studied systems, but the need to improve our understanding of dispersal in this context is well recognized (Kokko & Lopez-Sepulcre 2006).

Here we explore spatial mechanisms of density dependence and the role of dispersal using an extraordinarily detailed dataset on a formerly endangered tropical bird, the Mauritius kestrel *Falco punctatus* (Jones *et al.* 1995). Our study population was extirpated by the 1960s, but reintroduced at the end of the 1980s. Subsequent to its reintroduction, the population has grown, and has now become regulated at approximately 40 breeding pairs (Sutherland & Norris 2002). Since its inception, the

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population has been intensively monitored (Nicoll *et al.* 2003, 2004, 2006). The majority (more than 90%) of individuals entering the population are individually colour ringed at birth and the study area is a closed system—no colour-ringed immigrants have been recorded within the population, and no colour-ringed emigrants have been recovered or resighted elsewhere. This intensive monitoring programme means that we have, to date, complete, spatially referenced life histories for approximately 570 individual kestrels as the population has developed.

We used the kestrel data to test a series of predictions derived from the buffer effect process and focused on recruitment into the breeding population because we have previously shown evidence of density dependence in the demographic components of recruitment (Nicoll *et al.* 2003). First, the buffer effect predicts that the recruitment rates should vary between territories, and that this variation should reflect underlying spatial heterogeneity in territory quality. We tested this prediction by comparing recruitment rates between territories and developed more complex models to exclude environmental or individual quality as a potentially confounding effect. Additionally, we tested whether recruitment rates were density dependent within territories because multiple density-dependent mechanisms are possible within the same population (Rodenhouse *et al.* 2003). Second, the buffer effect predicts that poor quality territories should only be occupied at relatively high population densities, so we tested this prediction by relating the timing and duration of territory occupancy as the kestrel population has grown to territory-specific recruitment rates. Third, since patterns of occupancy may be modified by dispersal, we also estimated ideal occupancy according to the buffer effect theory, and compared this with the observed pattern. We also explored the extent to which occupancy patterns reflected the spatial positioning of territories as well as their quality. Finally, we used our analyses to describe the patterns of density-dependent recruitment generated by the buffer effect.

2. MATERIAL AND METHODS

(a) Study area and population data

The study was conducted in the Bambous mountain range in the east of Mauritius, Indian Ocean, which primarily consists of a single spine 15 km in length ranging in height from sea level to 626 m. The study area covers 163 km² encompassing a predominantly forested mountainous area and a buffer of agricultural land (almost exclusively sugar cane). Agricultural land extends for a considerable distance, to the extent that due to kestrels' short dispersal ability (Jones *et al.* 1995) it creates a dispersal barrier. Consequently, this population is a closed system. Habitat is heterogeneous with forested patches consisting of native forest in various stages of invasion by non-native tree and plant species including monotypic stands of invasive travellers palm *Ravenala madagascariensis* and plantations of *Eucalyptus globulus*. Dividing the forest are areas of open grassland created to provide grazing for introduced Java deer *Cervus timorensis*.

Since its inception, the Bambous mountains population has been intensively monitored (Nicoll *et al.* 2003, 2004, 2006). The majority of individuals entering the population are individually colour ringed at birth. Kestrels have a territory-based breeding system in which they defend an area

around the nest site, but routinely forage outside this defended area. Each breeding season territorial pairs are identified, and their breeding attempts monitored to establish the timing of egg laying, clutch size, brood size and the number of chicks fledged. Only a small number of birds have entered the breeding population as un-ringed individuals (Groombridge *et al.* 2001), mainly because of inaccessibility to a few nests (less than six by 1996) which meant that broods could not be ringed. In such cases, un-ringed birds entering the breeding population would be captured and colour ringed (so their subsequent life history could be documented), but their origin would be unknown. The small number of un-ringed individuals entering the breeding population is consistent with the number of inaccessible nests. Individuals are sexed based on field observations of breeding pairs and in the nest based on biometrics (Nicoll 2004), a method that has been validated by genetic analysis (Ewing 2005). Kestrels are single brooded, although a second clutch is laid on occasions, usually only if the first clutch or brood is completely lost.

A map of the study area showing the location of breeding sites and release sites used during the reintroduction programme is shown in figure 1.

(b) Statistical analysis

To investigate variation in recruitment rates between territories, we used a generalized linear mixed modelling (GLMM) framework implemented in the statistical program R (R Development Core Team 2007) and used the lme4 library (Crawley 2007). We first fitted a simple GLMM to the data, in which recruitment was modelled in relation to territory identity as a categorical fixed effect and female identity as a random effect. The response variable (recruitment rate) was defined as the number of fledged offspring subsequently entering the breeding population from a territory for each year it was occupied by a breeding pair. We initially assumed that the recruitment rate had a Poisson error distribution, but checked this assumption using the ratio of the residual deviance to the residual degrees of freedom. If this ratio was above 2, we refitted the model using quasi-Poisson errors. The significance of the territory fixed effect was assessed by comparison with a null GLMM that only included the mean recruitment rate and the female identity random effect.

Next we fitted a more complex GLMM to assess whether variation in recruitment rates between territories might be confounded by temporal variation in the environment or individual quality. For example, the recruitment rates associated with particular territories might have been relatively high because they happened to be occupied during favourable environmental conditions for recruitment, or by individual birds better able to produce recruits. Previous work has shown that rainfall at various times of the season adversely affects chick and post-fledging survival (Nicoll *et al.* 2003; Nicoll 2004); so we included a range of rainfall variables as fixed effects to quantify environmental quality. These included a categorical variable, describing whether the cyclone season was relatively 'wet' or 'dry' (which is related to post-fledging survival), and continuous variables for total June to September rainy days (which is related to the timing of breeding) and total December rainfall (which is related to chick survival in the nest). Definitions, details and data sources are given elsewhere (Nicoll *et al.* 2003; Nicoll 2004). Previous work has also shown that the quality of individual

Figure 1. Map of our study area in southeast Mauritius showing the location of breeding sites and sites used to release birds during the reintroduction programme. Crosses, release sites; open circles, breeding sites; grey shading, study area.

birds in terms of breeding success is strongly related to their past breeding experience (Nicoll 2004), so we included variables describing this trait (defined as the number of previous years recorded breeding) for male and female parents as fixed effects in the GLMM to quantify individual quality. We first fitted a maximal model containing all environmental and individual quality variables, and then simplified this model by progressively removing non-significant fixed effects until all fixed effects retained in the model were significant ($p < 0.05$). We then added the categorical variable describing territory identity as a fixed effect to this simplified model and assessed its significance. If territories vary in recruitment rates independent of variation in environmental or individual quality, we expected the territory identity fixed effect to remain significant.

We next used the simplified environmental and individual quality model to explore whether there was any evidence for density dependence in recruitment rates *within* the territories. To do this, we initially specified a GLMM containing the fixed effects from the simplified environmental and individual quality model above, and with territory identity as a random effect. We then compared the fit of this

model to an identical model to which density (measured as the number of breeding pairs) had been added as a fixed effect. If the density term is significant, then this implies density dependence in recruitment rates within the territories. This analysis was limited to territories that were occupied for more than three years, and those that had been occupied for at least one year prior to and after 1998 to ensure that each territory had experienced a range of densities.

All GLMMs were initially run using the recruitment rates that did not distinguish the sex of the recruits. Since it is possible that there may be sex-specific differences, we repeated the previous analyses separately on male and female recruits but the results were similar; so we only report the combined analysis for brevity. Mauritius kestrels often recruit in their first breeding season, but rarely when aged greater than two years, so recruitment rates were based on resighting data from all the years (1991–2005) but only included young fledged up to and including the 2003 cohort to allow sufficient time for surviving individuals to recruit into the breeding population. Nesting attempts were excluded from the analysis if they were managed as part of the reintroduction programme. We also repeated all our GLMM

analyses using alternative random effects structures to check whether our results were robust by fitting models based on male identity, and both female and male identities, but found similar results. For brevity, we only report the results based on models that included the female identity random effect.

The buffer effect theory predicts that the poorest quality kestrel territories in terms of recruitment rates should only be occupied relatively recently at high population densities. This means we would expect territories with the highest recruitment rates to have been occupied earlier and for longer as the kestrel population has grown, whereas territories with the lowest recruitment rates should have been occupied more recently and consequently for a shorter time period. To test these predictions, we first derived a mean recruitment rate for each territory from the GLMMs described above, and then fitted simple linear regression models in which mean recruitment rate for each territory was the predictor variable and either the year of first occupation or the number of years occupied was the response variable.

The previous analysis describes the observed patterns of territory occupancy in relation to quality (recruitment rate). We also estimated the ideal pattern we would expect to see if territory occupancy was solely determined by quality. To describe this ideal pattern we reordered the territory occupancy data such that the territory with the highest mean recruitment rate was associated with the highest number of years occupied recorded across all the territories in the dataset, the second highest mean recruitment rate with the second highest number of year occupied and so on for each territory. The regression of mean recruitment rate against the year of first occupation and the number of years occupied then describes the ideal relationship we would expect to see. We then compared the slopes of the ideal relationship with the slopes based on the observed data. Any significant differences would indicate a quantitative departure from the simple occupancy prediction based on the buffer effect theory.

Finally, we wished to estimate the patterns of density dependence in recruitment we would expect to see based on the observed and ideal patterns of territory occupancy. To do this, we assigned the mean recruitment rate for each territory to each year the territory was occupied. We then calculated the *per capita* recruitment rate for each year by summing the mean recruitment rates within a year across the territories and dividing the sum by the number of occupied territories. Next, we modelled the *per capita* recruitment rate for each year as a function of population density measured as the number of breeding pairs. We repeated this analysis for both the observed and ideal patterns of occupancy. In this way, we estimated the difference in density dependence between the observed data and the potential density dependence generated by ideal occupancy.

3. RESULTS

(a) Variation in recruitment between territories

The GLMM analysis showed highly significant variation in recruitment rates between territories ($\chi^2_{62}=127.9$, $p<0.0001$). The GLMM based on the environmental and individual quality variables showed that recruitment was significantly related to both environmental and individual qualities (table 1). Recruitment was significantly lower in relatively wet cyclone seasons, and increased significantly with the previous breeding experience of the male parent. When territory identity was

Table 1. Summary of minimum adequate GLMM of recruitment rates in relation to environmental and individual qualities. (June to September rainy days, December rainy days and female past breeding experience were terms removed during model simplification. The analysis included 301 observations from 53 territories.)

random effects	<i>n</i>	σ^2		
female ID	104	0.116		
fixed effects	estimate	s.e.	<i>z</i>	<i>p</i> -value
(intercept)	−0.411	0.137	−3.011	0.0026
wet (1) or dry (0)	−0.565	0.151	−3.732	0.0002
cyclone season				
male previous breeding experience (years)	0.089	0.036	2.500	0.0124

added to the model shown in table 1, it significantly improved the fit of the model to the data ($\chi^2_{53}=97.96$, $p=0.0002$), showing that variation in the recruitment rates between territories was unlikely to be confounded by environmental or individual quality. Note that fewer territories were available for this latter analysis due to incomplete data. We found no evidence of density dependence in the recruitment rates *within* the territories. The addition of density to the simplified environmental and individual quality GLMM, in which territory was included as a random effect, did not improve the fit of the model to the data (density fixed effect: $\chi^2_1=1.32$, $p=0.25$; $n=35$ territories).

(b) Territory occupancy

The mean recruitment rates for individual territories ($n=63$) varied between 0 and 1.55 recruits per breeding pair per cohort. Mean recruitment rates for territories estimated by the simple GLMM (with female identity as the random effect) only including territory identity compared with that based on the environmental and individual quality variables in addition to territory identity were very similar (linear model: $r^2_{\text{adj}}=97.3\%$; intercept = 0.00018 ± 0.013 (mean $\pm$ s.e.), $p=0.99$; slope = 0.96 ± 0.022 , $p<0.0001$). Consequently, we used the output from the simple GLMM in subsequent analyses.

Regression analysis showed a significant negative relationship between the mean recruitment rate for each territory and the year of first occupancy (figure 2a), and a significant positive relationship with the number of years occupied (figure 2b). This suggests that higher quality territories in terms of recruitment rates were occupied earlier and for longer as the population grew, compared with lower quality territories that were occupied later at higher population densities. This is in qualitative agreement with predictions from the buffer effect. Interestingly, the analysis of the ideal occupancy data suggests that higher quality territories were actually occupied slightly later and for less time than would be expected based on ideal occupancy, whereas the reverse was true for low-quality territories (figure 2). Therefore, although our analysis is qualitatively in agreement with the buffer effect, occupancy departs quantitatively from expectations.

Figure 2. (a) The year of first occupancy and (b) the number of years occupied for each territory in relation to its mean recruitment rate. The relationship in (a) is described by the linear model: $y = 1996.94 - 3.567 \times (R^2_{\text{adj}} = 13.8\%, p = 0.0016)$. The relationship in (b) is described by the linear model: $y = 4.195 + 7.01 \times (R^2_{\text{adj}} = 41.1\%, p < 0.0001)$. The linear relationship for ideal occupancy is shown on each plot as a dashed line and is significantly different from the observed relationship (solid line) for the year of first occupancy (ideal slope = -5.569 ; observed slope = -3.567 ± 2.157 (mean $\pm$ 95% CIs)) and the number of years occupied (ideal slope = 10.47 ; observed slope = 7.01 ± 2.108).

To investigate the role of dispersal in this departure, we performed an additional analysis of the observed occupancy data. If dispersal is restricted in scale with respect to the size of the study area, then the discrepancy between observed and ideal occupancy might arise if territories close to the expanding breeding population are occupied sooner than those further away. To test this possibility we repeated the analysis of the year of first occupancy and the number of years occupied, including the mean recruitment rate for each territory and its distance from the nearest release site as predictor variables in multiple regression models. Releases were undertaken at 13 sites within our study area (figure 1), and we hypothesized that if dispersal is restricted, territory occupancy over time should be related to minimum distance from the closest of these sites. The analysis showed that both mean

Table 2. Multiple linear regression analysis of (a) the year of first occupancy and (b) the number of years occupied in relation to the mean recruitment rate for each territory and its distance to the nearest release site.

independent variable	estimate	s.e.	p-value
(a)			
constant	1994.799	0.863	<0.0001
mean recruits per territory	-2.345	1.066	0.0317
nearest release site	1.179	0.356	0.0016
(b)			
constant	5.128	0.773	<0.0001
mean recruits per territory	5.145	0.955	<0.0001
nearest release site	-0.899	0.319	0.0066

Figure 3. Patterns of density-dependent recruitment estimated using observed and ideal patterns of occupancy. The ideal relationship, shown as a dashed line, is described by the linear model: $y = 1.17 - 0.0145 \times (R^2_{\text{adj}} = 92.9\%, p < 0.0001)$. The observed relationship, shown by a solid line, is described by the linear model: $y = 0.8 - 0.0067 \times (R^2_{\text{adj}} = 77.8\%, p = 0.0002)$. Density refers to the number of breeding pairs.

recruitment rate and distance to the nearest release site were significant predictors of the timing and duration of territory occupancy (table 2).

(c) The strength of density dependence

The observed and ideal patterns of occupancy generated significantly different patterns of density-dependent recruitment (figure 3). Recruitment declines significantly more rapidly under ideal territory occupancy (slope = -0.0145 ± 0.0025 ($\pm$ 95% CI)), compared with observed territory occupancy (slope = 0.0067 ± 0.0022). At low population densities, *per capita* recruitment rates were up to approximately 1.5 times as high under ideal occupancy compared with the observed data, whereas at high density *per capita* recruitment rates were comparable. These results show that restricted dispersal can reduce the strength of density dependence due to constraints on territory occupancy with respect to territory quality.

4. DISCUSSION

Our results contribute to the growing body of evidence showing that spatial processes can play an important role in density dependence and population regulation in the wild (examples cited in §1). More importantly, however, our results additionally show that the use of space and its consequences for density dependence can be modified by dispersal. Specifically, we show that restricted dispersal can significantly reduce the strength of spatial density dependence, a finding that has important implications for population dynamics and population responses to environmental change.

These broad conclusions rest upon the validity of our analyses, particularly the extent to which variation in recruitment rates between territories can be regarded as reflecting the underlying spatial heterogeneity in territory quality. It is possible that differences between territories instead reflected variation in environmental conditions when the territories were occupied, or the quality of individual birds occupying territories. We consider this possibility unlikely. While we documented significant effects of environmental and individual qualities on recruitment rates, we found no evidence that differences in recruitment rates between territories were confounded by these effects. We show that recruitment was significantly lower in years with a relatively wet cyclone season, which occurs during the immediate post-fledging period. This finding is consistent with our previous work that showed reduced post-fledging survival probabilities under similar conditions (Nicoll *et al.* 2003), which is likely to reflect difficult foraging conditions for inexperienced juveniles when rainfall is frequent. We also show that recruitment rates significantly increase as the previous breeding experience of the male increases. Males feed their mates and play a main role in food provisioning for their offspring while in the nest and immediately post fledging (Nicoll 2004). There is extensive evidence in birds that the quality of parental care, and hence breeding success, increases with previous breeding experience (Daunt *et al.* 2007; Nevoux *et al.* 2007). Despite these effects, the territory-specific recruitment rates estimated using a model only including territory identity generated values almost identical to those estimated by a model that accounted for environmental and individual qualities. This suggests that territory differences are unlikely to be confounded by environmental or individual quality.

Variation in recruitment rates between territories is likely to reflect the underlying spatial heterogeneity in territory quality. This spatial heterogeneity is likely to be determined by variation in nest site quality, or the quality of habitat surrounding the nest site. Kestrels nested in natural cavities in cliffs and trees, as well as in nest boxes that were erected in the early years of the reintroduction programme (Jones *et al.* 1995; Nicoll *et al.* 2003); approximately 60% of nesting attempts occurred in boxes over the study period. Previous work has shown that natural cavities have lower pre-fledging survival rates than nest boxes due to elevated risks of predation and flooding during rainfall (Nicoll 2004). Habitat surrounding the nest site is likely to affect food availability through its impact on the distribution and abundance of day geckos, the principal prey of Mauritius kestrels (Jones 1987; Jones *et al.* 1995). Although recent work has documented gecko distribution in certain Mauritian forest

habitat types (Harmon *et al.* 2007), data on food availability with respect to habitat are largely lacking. A more comprehensive analysis of the potential causes of spatial heterogeneity in relation to nest sites and habitats will be published elsewhere.

Our results clearly show patterns of territory occupancy which are consistent with expectations from the buffer effect. Territories with relatively high recruitment rates were occupied early in the study period, when population density was relatively low, and have been occupied relatively consistently since. By contrast, territories with relatively low recruitment rates were only occupied relatively recently, when population density was relatively high. Furthermore, we show that this pattern of occupancy generates density dependence in recruitment. Note that our results are consistent with the habitat heterogeneity hypothesis in which density dependence in vital rates is generated solely by the occupancy of territories that vary in quality rather than the individual adjustment hypothesis in which density dependence in vital rates is generated by density dependence in vital rates *within* territories because we only found evidence of density dependence in recruitment due to territory occupancy patterns, rather than density-dependent changes in recruitment within territories (Both 1998; Rodenhouse *et al.* 2003; Sillett *et al.* 2004). In these respects, our results contribute to the growing body of work, which shows that spatial density dependence is a potentially important mechanism of population regulation in the wild. The novel finding in our study is that restricted dispersal significantly reduces the strength of density dependence generated by the buffer effect. We show that territory occupancy was influenced both by territory quality (recruitment rate) and a territory's distance from a release site. Territories close to release sites were occupied sooner and for longer during the population's development than territories further away. This resulted in a significant difference between the observed and ideal patterns of territory occupancy. Although this difference is subtle (figure 2), it is sufficient to reduce the rate at which *per capita* recruitment declines with increasing population density by approximately 50%, and means that *per capita* recruitment is, on average, lower than it could be (figure 3). This can be considered as the population-level cost of restricted dispersal. While it is widely recognized that dispersal and its consequences are theoretically important for our understanding of spatial processes and the extent to which individual decisions can generate population-level costs (Kokko & Lopez-Sepulcre 2006), our study is one of the first to quantify such a cost in the wild.

Our results have important implications for population dynamics and for our understanding of population responses to environmental change. In broad terms, the reduction in the strength of density dependence due to restricted dispersal also reduces the extent to which spatial processes buffer the population against perturbation (Turchin 1999). However, this simple conclusion masks the importance of understanding the spatial dynamics of environmental change. When dispersal is restricted, the impact of any environmental change that alters the pattern of spatial heterogeneity (e.g. habitat degradation) or the spatial distribution of individuals (e.g. mortality events) will depend on the precise spatial pattern of change. This is because the demographic consequences of

environmental change will be dictated by the way dispersal reshapes distribution patterns. This argues for the development of mechanistic models of population dynamics, incorporating spatial processes with dispersal, which can then be used for forecasting population responses to environmental change (Stephens *et al.* 2002). It also argues against a phenomenological approach to density dependence which is typical of current population viability models (Henle *et al.* 2004). Our results also have implications for the design of reintroduction programmes because where dispersal is restricted it will be important to have multiple release sites throughout a potential range in order to ensure individuals are able to occupy high-quality sites as quickly as possible.

Populations recovering from relatively low density, including the Mauritius kestrel, provide ideal model systems for understanding spatial processes and their population consequences in the wild. These systems are also ideal for developing and testing mechanistic population models based on spatial processes. Although there is a growing recognition of the value of such systems for addressing basic ecological questions (Sarrazin & Barbault 1996; Armstrong *et al.* 2005), better integration between applied and basic ecology is still needed. Studies initiated for applied reasons rarely consider the wider basic ecological value of the data being collected, though they should do so. Basic ecologists need to recognize that such studies can provide general insights into the mechanisms of density dependence, which may allow them to reconstruct population-level patterns for study systems in which the direct observation of density dependence is difficult.

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