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Changes in intrapopulation resource use patterns of an endangered raptor in response to a disease-mediated crash in prey abundance

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Summary

1. A long-standing question in ecology is how natural populations respond to a changing environment. Emergent optimal foraging theory-based models for individual variation go beyond the population level and predict how its individuals would respond to disturbances that produce changes in resource availability.

2. Evaluating variations in resource use patterns at the intrapopulation level in wild populations under changing environmental conditions would allow to further advance in the research on foraging ecology and evolution by gaining a better idea of the underlying mechanisms explaining trophic diversity.

3. In this study, we use a large spatio-temporal scale data set (western continental Europe, 1968–2006) on the diet of Bonelli's Eagle *Aquila fasciata* breeding pairs to analyse the predator trophic responses at the intrapopulation level to a prey population crash. In particular, we borrow metrics from studies on network structure and intrapopulation variation to understand how an emerging infectious disease [the rabbit haemorrhagic disease (RHD)] that caused the density of the eagle's primary prey (rabbit *Oryctolagus cuniculus*) to dramatically drop across Europe impacted on resource use patterns of this endangered raptor.

4. Following the major RHD outbreak, substantial changes in Bonelli's Eagle's diet diversity and organisation patterns at the intrapopulation level took place. Dietary variation among breeding pairs was larger after than before the outbreak. Before RHD, there were no clusters of pairs with similar diets, but significant clustering emerged after RHD. Moreover, diets at the pair level presented a nested pattern before RHD, but not after.

5. Here, we reveal how intrapopulation patterns of resource use can quantitatively and qualitatively vary, given drastic changes in resource availability.

6. For the first time, we show that a pathogen of a prey species can indirectly impact the intrapopulation patterns of resource use of an endangered predator.

Key-words: *Aquila fasciata*, diet variation, emerging infectious disease, foraging theory, *Oryctolagus cuniculus*, rabbit haemorrhagic disease, territory, western Europe

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Introduction

A long-standing question in ecology is how natural populations respond to a changing environment. The optimal foraging theory (OFT; Pyke, Pulliam & Charnov 1977; Stephens & Krebs 1986) helps address this question by generating predictions on how populations should respond when facing different levels of food resource availability. For instance, when resource availability is high, the OFT predicts narrow diets because individuals specialise in preferred resources. Conversely, when resource availability lowers, diets may expand as individuals add suboptimal resources to fulfil their energetic demands. Such predictions imply the underlying assumption that individuals within populations respond similarly to variation in the availability of food resources. However, recent studies have repeatedly demonstrated that increased population diet breadth may occur via increasing intrapopulation or inter-individual diet variation instead of an average increase in individuals' diet breadth (Bolnick *et al*. 2007; Svanbäck & Bolnick 2007). Nevertheless, response at the individual level may vary depending on how individuals rank their prey, which, in turn, results in different resource use patterns (Svanbäck & Bolnick 2005; Araújo *et al*. 2010; Pires *et al*. 2011). Evaluating such variations in resource use patterns within wild populations under changing resource availability conditions provides an opportunity to test theoretical predictions and to further advance in the research on foraging ecology and evolution.

Models based on the OFT (Svanbäck & Bolnick 2005) that formally established the connection between intrapopulation diet variation and resource availability provide a useful framework to link resource use patterns to possible underlying mechanisms. Such models represent a few examples of the possible rules that describe how individual niches vary with resource availability. The shared preferences model (SPm), for instance, describes a situation where all the individuals have the same prey preferences, but they differ in their ability to handle them. Therefore, when resource availability is high, all the individuals feed on the preferred prey, but as resource availability decreases, individuals begin to include alternative prey in their diet in a similar order, but at different times. If resource availability decreases further, all the prey become scarce, and individuals expand their diets and tend to consume all the prey. In the competitive refuge model (CRm), the preferred prey is also the same, but the order of preference of the alternative prey differs among individuals. This model predicts a similar behaviour to the SPm of all the individuals for low and high resource availability. At intermediate resource availability levels, however, individual diets overlap less, and the population niche breadth is wider. Finally, when the preference order of all the prey is different, the population falls into a distinct preferences model (DPm). In this situation, individuals are highly selective in their preferred prey type when resource availability is high and become less selective in environments with low resource availability.

By linking recently developed metrics borrowed from the physics of complex networks and inter-individual variation studies in a classical OFT framework (Araújo *et al*. 2008, 2010; Pires *et al*. 2011), here we take advantage of a large-scale spatio-temporal data set on an endangered territorial predator's diet to understand how intrapopulation resource use patterns change in response to a crash in the population of its main prey. We analyse the long-term changes in the diet of the Bonelli's Eagle (*Aquila fasciata* Vieillot, 1822) population in western continental Europe over the last four decades. Bonelli's Eagle is one of the most threatened birds of prey in Europe (BirdLife International 2004). Scarcity of trophic resources has been identified as one of its main threats on the continental scale (Real 2004). This raptor bases its diet on rabbits (*Oryctolagus cuniculus* Linnaeus, 1758), although other similar-sized prey such as birds (e.g. partridges or pigeons) and reptiles (e.g. lizards) also become important where and when they are abundant and the rabbit scarce (Moleón *et al*. 2009). At the end of the 1980s and the beginning of the 1990s, a major, widespread outbreak of rabbit haemorrhagic disease (RHD) in western Europe resulted in a drastic reduction (of *c*. 50–80%) and fragmentation of the rabbit population (Virgós, Cabezas-Díaz & Lozano 2007; Moleón, Almaraz & Sánchez-Zapata 2008). This disease-mediated drop in the eagle's main prey availability triggered an increase in its trophic diversity at the population level, as rabbits lost representation in its diet (Moleón *et al*. 2009). Such an increase in trophic diversity is predicted by the classic foraging theory: as the abundance of preferred resources diminishes, predators include suboptimal resources. The central question now is how Bonelli's Eagles responded at the intrapopulation level. Answering this question would allow us to gain a better idea of the underlying mechanisms explaining trophic diversity.

Our general aim here is to explore how an emerging infectious disease (EID) – RHD – causing the availability of the main prey – rabbits – to dramatically drop, impacted on resource use patterns of the predator – Bonelli's Eagle. For this purpose, we describe how intrapopulation resource use patterns changed over time. In our system, the predator's territorial behaviour (Bosch *et al*. 2010) allows us to partially control for conspecific competition for prey. This offers us a rare opportunity to disentangle the intrapopulation and population dietary effects of disease-mediated variations in resource availability. According to Svanbäck and Bolnick's models' predictions and to the empirical background (Moleón *et al*. 2009), we might expect different outcomes to the eagle population niche unleashed by the rabbit population breakdown. If all individuals within the population shared the same rank preference order with different acceptance rate for alternative resources, the diet of those individuals that were less prone to include alternative prey in their diets would become subsets of the diets of the less selective individuals; thus, a nested pattern in the diets would emerge (Araújo *et al*. 2010; Pires *et al*. 2011). Alternately, if individuals had a different rank order for

alternative prey, we should expect more or less discrete groups of individuals sharing similar prey (CRm). The third theoretical scenario, the DPm, is not applicable to our case because of Bonelli's Eagle's well-known preference for rabbits (e.g. Moleón *et al.* 2009, 2012).

Materials and methods

DATA SAMPLING

As all the information about Bonelli's Eagle's diet in the study area is detailed by territories at best, we did all the analyses using breeding pair as the analytical unit. In favour of this, both sexes within pairs have been suggested to show similar behaviour and foraging patterns (Real 1982; Bosch *et al.* 2010; R. Bosch, J. Real, A. Tintó, E.L. Zozaya, C. Castell & M. Moleón, personal observation). The diet data sampling method has been described in detail in Moleón *et al.* (2009). Briefly, we compiled information on the breeding (February–June) diet in Bonelli's Eagle territories in Portugal, Spain and France spanning the 1968–2006 period. Only the data employing intensive direct observations or those analysing regurgitated pellets' content (Real 1996), as well as territories providing ≥20 prey items (see Jovani & Tella 2006), were used. All the study years in each period (before vs. after RHD) were pooled together for each territory. The final sample size was 44 territories before and 81 after the RHD outbreak. The date when RHD irrupted in each locality was estimated from the scientific and technical literature. Prey species were grouped into the following seven categories: rabbit, other mammals, partridges (mainly *Alectoris rufa* Linnaeus, 1758), pigeons, corvids, other birds and herptiles (mainly *Timon lepidus* Daudin, 1802). We calculated the contribution of each prey group to the diet of each eagle pair as its frequency of occurrence (% *N*) in relation to total prey items.

DATA ANALYSES

All analyses were performed for the periods before and after RHD separately. We used a recently developed framework based on complex network theory that characterises patterns and identifies changes in diet at the individual (breeding pair in our case) level (Araújo *et al.* 2008, 2010). For all the analyses, we adopted the approach described in Araújo *et al.* (2010), where a more detailed explanation of the indices used can be found.

Diet variation between pairs

We used index E to calculate the degree of variation in diet at the breeding pair level (Araújo *et al.* 2008). Contrary to other analogous indices, this has known statistical properties and is based on the diet overlap between pairs instead of on the overlap between pairs and the whole population. E ranges from 0 (the diets of the two pairs are identical) to 1 (diets are completely different). As diet variation can also result from forager passive sampling with individuals randomly sampling a shared distribution of resources, we compared the calculated E with a null distribution of E-values (see below the 'Null model' section). Null model and E calculations were performed using MATLAB 7.4 (Mathworks, Natick, MA, USA). We checked the reliability of our sample sizes by testing the effects of reduced number of pairs in E. We used a rarefaction approach with 1000 replicates for 95%, 90%, 85%,… and 25% of the total sampling effort. If sampling size highly affects a given metric, we would expect that simulations of smaller sampling effort to produce large effects on the metric value.

Clustering

To study the clustering of individuals' diets, we combined measure E with clustering index C_{ws} (see Fig. 1 in Araújo *et al.* 2010 for a graphic explanation of the interpretation of these indices). This provides more detailed information about the organisation patterns of resource use within populations. C_{ws} varies between −1 and +1. It is positive and approaches +1 when the diet variation between pairs is clustered, and it is negative and tending to −1 when diet variation is continuous. If there is no diet variation, then both E and $C_{ws} \to 0$. If diet variation is continuous (i.e. there is little niche overlap between pairs), $E \to +1$ and $C_{ws} \to -1$. If diet variation is discrete (i.e. pairs form dietary groups), then both E and $C_{ws} \to +1$. If the diets in the pairs with more restricted diets are ordered subsets of the diets in the generalist pairs, then $E \to +1$ and $C_{ws} \to 0$. Clustering significance was tested by comparing the calculated values with a null distribution of C_{ws} values. We used DIETA 1.0 (Araújo *et al.* 2008) to calculate the index and to perform simulations. We also performed the rarefaction analysis to test the sampling effort for C_{ws}.

Null model

As our samples come from different regions in Europe (Moleón *et al.* 2009), diet variation might correspond to regional spatial variation in resource availability. If this is true, when trying to evaluate the significance of individual variation metrics, we could find differences that correspond solely to such regional differences in resource availability. As our diet data relate to the nests found in specific regions, we used this information to perform a preliminary test to check whether the geographic structure of our data could affect our estimates of diet variation and resource use patterns. To do this, we employed the dietary overlap measure w_{ij} used to calculate index E of inter-pair variation ($E = 1-\text{sum}\ (w_{ij})$). Weights vary from 0 to 1 ($0 \le w_{ij} \le 1$) as a measure of the pairwise diet overlap between individuals i and j, 0 indicating no diet overlap and 1 denoting total overlap. Then we used the Kruskall–Wallis test to test for differences in the pairwise dietary overlap of those breeding pairs that were sampled in the same geographic area and pairs sampled in different areas. If spatial heterogeneity in prey availability had affected predator's dietary variation, we would expect those pairs sampled in the same geographic area to present more similar diets than those pairs from different areas.

As the preliminary analysis mentioned earlier indicated that the diets of pairs in the same region were more similar than diets of pairs from different regions, we built a null model that explicitly accounted for spatial variation. By doing that, the theoretical diet matrices generated by the model also incorporate regional differences, and thus any differences between the observed value and the values obtained for the model simulations are not only a consequence of such regional differences. In this model, the diet distribution of a given regional subpopulation was defined as the average diet of pairs sampled within that region (see Bolnick *et al.* 2002). Then each pair was reassigned a new diet (with the same number of prey items as was observed for that pair) randomly drawn via multinomial sampling from the corresponding regional subpopulation diet distribution (Bolnick *et al.* 2002). By calculating E for each theoretical population generated by this model (we used 1000 iterations), the null hypothesis can be rejected if E is over 95% of the null E values. Similarly, for C_{ws}, the null hypothesis is rejected whenever the observed value falls outside the interval containing the central 95% null C_{ws} values. As the number of sampled territories before and after RHD differed, we also report relative E and C_{ws} values. Relative values were calculated as the difference between the observed value and the values predicted

for randomised diets (e.g. $E^* = (E - E_{random})/E_{random}$). This relative metrics controls for the possible effects of different sampling size, allowing comparisons to be made among data sets (i.e. before and after RHD).

Nestedness

The diet data of the breeding pairs can be described by a binary matrix where each row represents a different prey item and each column represents a different pair. In this matrix, cells $a_{ij} = 1$ when prey i is used by the breeding pair j and 0 otherwise. This matrix can be used to qualitatively study the nestedness of the diet information. There has been much debate about the best metrics to analyse nestedness (Ulrich & Gotelli 2007; Almeida-Neto *et al.* 2008; Ulrich, Almeida-Neto & Gotelli 2009). In this study, we used the *NODF* metrics (acronym for the nestedness metrics based on overlap and decreasing fill; Almeida-Neto *et al.* 2008) using the ANINHADO software (Guimarães & Guimarães 2006). This metrics has been identified as being good for any type of analyses in nestedness (Ulrich, Almeida-Neto & Gotelli 2009). *NODF* values near 100 represent highly nested diets, while values close to 0 and the intermediate, respectively, arise from other non-random patterns and random patterns of resource use. To evaluate the significance of nestedness, we compared the *NODF* of the diet matrix with the *NODF* of 1000 simulated matrices using a null model. Here presences are randomly assigned to any cell within the matrix, and the probability that cell a_{ij} shows a presence is $(P_i/C + P_j/R)/2$, in which P_i is the number of presences in row i, P_j is the number of presences in column j, C is the number of columns and R is the number of rows. As nestedness may also appear as a result of reduced sampling effort, we performed a rarefaction analyses similar to that described for E.

As the size of the matrices differed between periods (i.e. before and after RHD), we also compared the degree of nestedness before and after RHD using a standardised effect size (SES) of the *NODF* value (Ulrich & Gotelli 2007). This measure indicates the number of standard deviations that the observed index is above or below the mean index of simulated matrices (Gotelli & McCabe 2002). We calculated the SES as a Z score ($NODF^*$ = (observed *NODF*−mean simulated *NODF*)/SD simulated *NODF*).

Results

After the major RHD outbreak in western Europe, substantial changes in the diet patterns of Bonelli's Eagle at the breeding pair level occurred (Table 1). As shown by the pairwise diet overlap comparison, even if raw E values seemed to suggest that pair diets were more variable before RHD, the relative values (E^*) indicated that the difference between the observed degree of inter-pair variation and the degree that was expected by chance was larger after the outbreak than it was before. Along the same lines, the clustering analysis suggested that there were no clusters of pairs with similar diets before RHD, but such clustering was much higher after RHD than expected by chance. As the null model controlled for geographic variation in resource availability, clustering did not relate to large-scale spatial variation. The nestedness analysis revealed that diet at the pair level presented a nested pattern before RHD, but not after (Fig. 1). Sample size did not affect the outcome of any of the calculated indices (see Fig. S1, Supporting information).

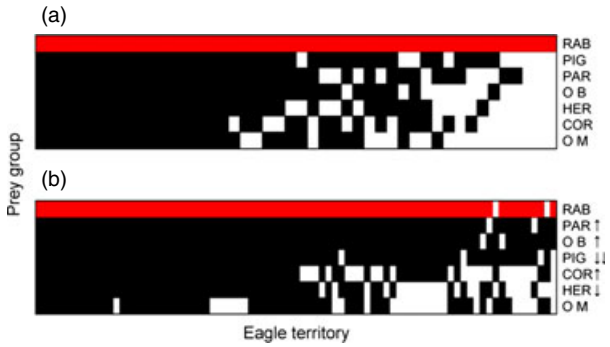

Fig. 1. Matrices describing resource use by Bonelli's Eagle pairs in breeding territories before (a) and after (b) the major rabbit haemorrhagic disease (RHD) outbreak. When prey i is used by the pair of territory j, the a_{ij} cell becomes filled. RAB, rabbit; PIG, pigeons; PAR, partridges; OB, other birds; HER, herptiles; COR, corvids; OM, other mammals. The direction and number of arrows, respectively, indicate direction and magnitude (number of rows) of the relative change in the position of each prey group in the matrix after RHD.

Discussion

Here, we show how intrapopulation resource use patterns can vary under dramatic changes in ecological conditions, that is, resource availability (see Tinker, Bentall & Estes 2008). Figure 2 schematises and integrates the main variations in Bonelli's Eagles' diet diversity and organisation at

Table 1. Measures of intrapopulation – breeding pairs – diet variation (E), clustering (C_{ws}) and nestedness (*NODF*) for the Bonelli's Eagle population in W Europe before and after the major rabbit haemorrhagic disease (RHD) outbreak

	E	E^*	C_{ws}	C_{ws}^*	*NODF*	*NODF**
Before RHD	0·4643***	0·22	$-0·0017^{NS}$	−0·74	73·18*	1·48
After RHD	0·3914***	0·30	0·0301***	2·32	$68·58^{NS}$	1·21

NS, not significant.
E ranges between 0 and 1 and higher values represent greater variation in diet between pairs; C_{ws} measures the clustering degree, ranging from −1 (continuous values) to 1 (clustered); *NODF* evaluates the degree of nestedness of the pair's diets and values vary from 0 (no nestedness) to 100 (perfect nestedness); E^*, C_{ws}^* and *NODF**, respectively, represent the transformed values of E, C_{ws} and *NODF* to account for the differences in the number of samples and to compare between the eagle's diet before and after RHD.
$^*P < 0·05$; $^{***}P < 0·001$.

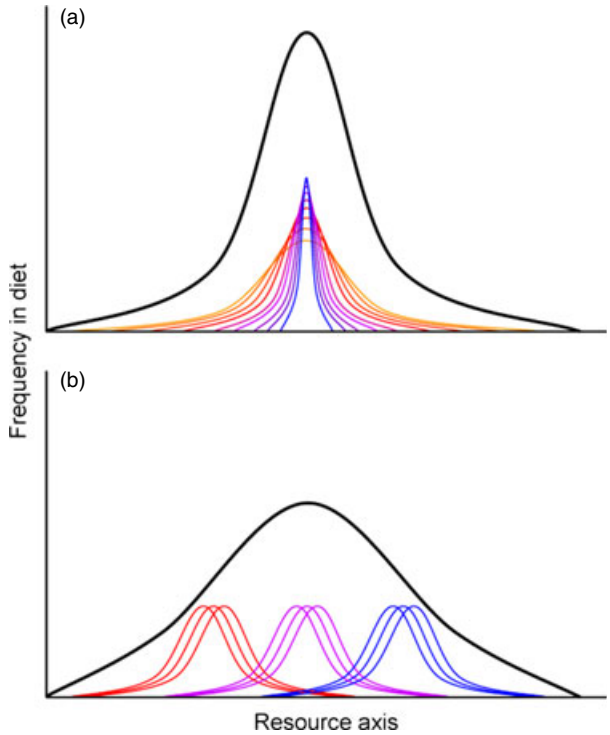

Fig. 2. Conceptual representation of changes in diet diversity and organisation on both the intrapopulation and population scales of Bonelli's Eagle in western continental Europe before (a) and after (b) the major rabbit haemorrhagic disease (RHD) outbreak. Diet at the population level (thick, black lines) included less proportion of the staple prey – rabbit – and consequently diversified after the rabbit outbreak (Moleón *et al.* 2009). Pair diets (thin, coloured lines) before RHD were nested around rabbit consumption (as indicated by *NODF* results; see Table 1 and Fig. 1); after RHD (non-geographically related), pairs grouped in weak clusters focused on the same alternative prey (as indicated by C_{ws}* results; see Table 1). Thus, the main prey is now consumed at lower frequencies than before RHD on average. Note that the pattern of individual resource use became more heterogeneous after the outbreak (as suggested by E* values; see Table 1).

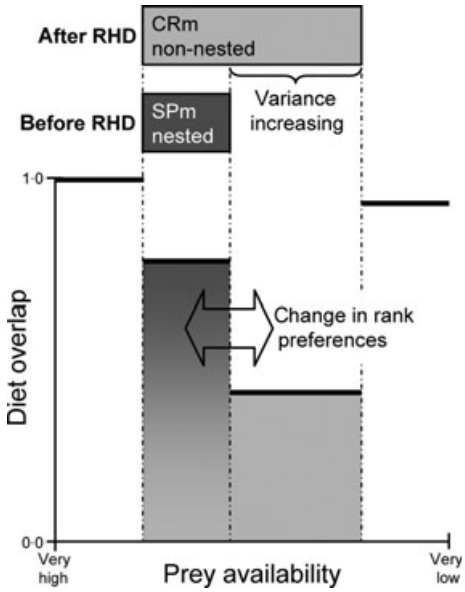

Fig. 3. A potential interplay between prey availability and preference models in determining resource use patterns. The figure shows the transition from a 'shared preferences model' (SPm) to a 'competitive refuge model' (CRm) within a range of preferred prey intermediate densities. At relatively high prey density consumers would share rank preferences, showing nested diets. However, as prey density decreased, breeding pairs would change their rank preferences, breaking the nested pattern and reducing diet overlap. Within the range of rabbit densities found before rabbit haemorrhagic disease (RHD), Bonelli's Eagle pairs faced relatively high, medium and low rabbit densities, depending on the territory; after RHD, different inter-territorial rabbit densities were also found, but rabbit density average and variance decreased and increased, respectively. This variability in the prey densities territories that were exposed to both before and after RHD allowed us to identify inter-pair variation patterns separately for each period. In grey is depicted the main rabbit density range found before (dark grey) and after RHD (light grey); note that rabbit abundance in the relatively high prey density period studied here was not at its maximum because of the impact of another outbreak caused by myxomatosis four decades before RHD irruption (Fenner & Fantini 1999). See text and Svanbäck & Bolnick (2005) for more details on the models.

both the population and breeding pair scales, and at both ranges of prey availability (i.e. before and after RHD). For the first time, we explore the way in which a pathogen (an EID) of a prey species can indirectly impact the consumer's intrapopulation resource use patterns. Before RHD, Bonelli's Eagles' diet in W continental Europe was nested, in such a way that pairs with narrower diets ate a subset of prey items of the pairs with broader ones. In general, this is in agreement with the predictions of a model that assumes pairs in all the territories displaying the same rank preferences (SPm), with rabbits being the first-ranked prey (which agrees with previous evidence for Bonelli's Eagle prey preferences on both large and small scales, e.g. Moleón *et al.* 2009, 2011, 2012). Strikingly after RHD, however, this resource use pattern switched both quantitatively and qualitatively, moving from a situation that is consistent with a theoretical scenario in which eagles shared their rank preferences to another scenario in which each pair presented different rankings for less preferred prey (CRm; see Fig. 3; Svanbäck & Bolnick 2005). Hence, our findings indicate that contrasting patterns of resource use may emerge in a single population under changing environmental conditions, that is, differential preferred prey density ranges (as previously suggested by Araújo *et al.* 2010 for a tropical system where resources change seasonally).

Two non-mutually exclusive OFT-based mechanisms could explain why eagles' rank preferences diverged at the breeding pair level. As energetic demands became more difficult to satisfy when rabbit populations dropped, eagles were surely forced to increase their foraging efforts (Moleón *et al.* 2009). Main prey scarcity could then bring to light latent differential inter-pair phenotypic abilities to exploit distinct prey, including differential capture success and consumption and digestion efficiency (Bolnick *et al.* 2003, 2007; Svanbäck & Bolnick 2005; Tinker, Bentall & Estes 2008), as well as behavioural diversification in microhabitat use (Kobler *et al.* 2009). On the other hand, local (territorial) spatial heteroge-

neity in resource availability may also have contributed. Previous evidence has suggested that RHD altered the density distribution pattern of not only rabbits (Villafuerte *et al*. 1995; Calvete 2006), but also other sympatric prey indirectly via hyperpredation processes (Moleón, Almaraz & Sánchez-Zapata 2008; Moleón *et al*. 2009). In accordance with the RHD epidemiology (Calvete 2006), the disease outcome on rabbit population dynamics was highly unpredictable in areas of a medium carrying capacity of rabbits, which characterised most of the Bonelli's Eagle's range. Thus, we would expect eagle territories to have a very variable prey composition and abundance after RHD if compared with before the outbreak, and this could be subsequently reflected in eagle pair diets.

Our findings further support the idea that diet variation at the intrapopulation level is a widespread phenomenon in nature (Bolnick *et al*. 2003; Araújo, Bolnick & Layman 2011), especially at upper trophic levels (Araújo, Bolnick & Layman 2011). In addition, in the absence of strong disruptions (i.e. before RHD), in our system, we found a nested pattern in the predator–prey trophic interactions on the scale of breeding pairs. This is in agreement with the suggestion of nestedness as a general pattern in individual-level trophic interactions (Pires *et al*. 2011). Araújo, Bolnick & Layman (2011) recently provided a comprehensive list of guidelines for future research into the study of individual diet variation. In addition to their recommendations, our findings highlight the importance of seizing the opportunity of 'natural experiments' to explore individual responses to environmental changes. Equally, territorial animals appear to be proper study models to test predictions derived from intraspecific competition models (Svanbäck & Bolnick 2005) and the ideal free distribution theory (Fretwell & Lucas 1970).

Finally, EID-mediated disruptions of resource use patterns on large spatio-temporal scales have proved to occur at levels ranging from individuals (this study) to populations (Moleón *et al*. 2009) and communities (Moleón, Almaraz & Sánchez-Zapata 2008). In light of the few empirical studies available, there is evidence for an important influence of genetics on individual diet variation (Araújo, Bolnick & Layman 2011), at least for some foraging components (Gibbons, Ferguson & Lee 2005; Latshaw & Smith 2005). Hence, EIDs may not only pose an emergent threat for biodiversity through the alteration of the normal ecological processes at multiple levels of life organisation, but might also become an efficient driver of evolution. The study of intrapopulation variation in different ecological scenarios can reveal how individuals adapt to variations in environmental conditions and provide outstanding answers to ecologists, evolutionary biologists and conservation biologists concerned about the future of a human-aided changing world.

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Supporting information

Additional supporting information may be found in the online version of this article:

Fig. S1. Rarefaction of sampling effort for dietary data before and after the RHD outbreak and its effects on E, C_{ws} and $NODF$.

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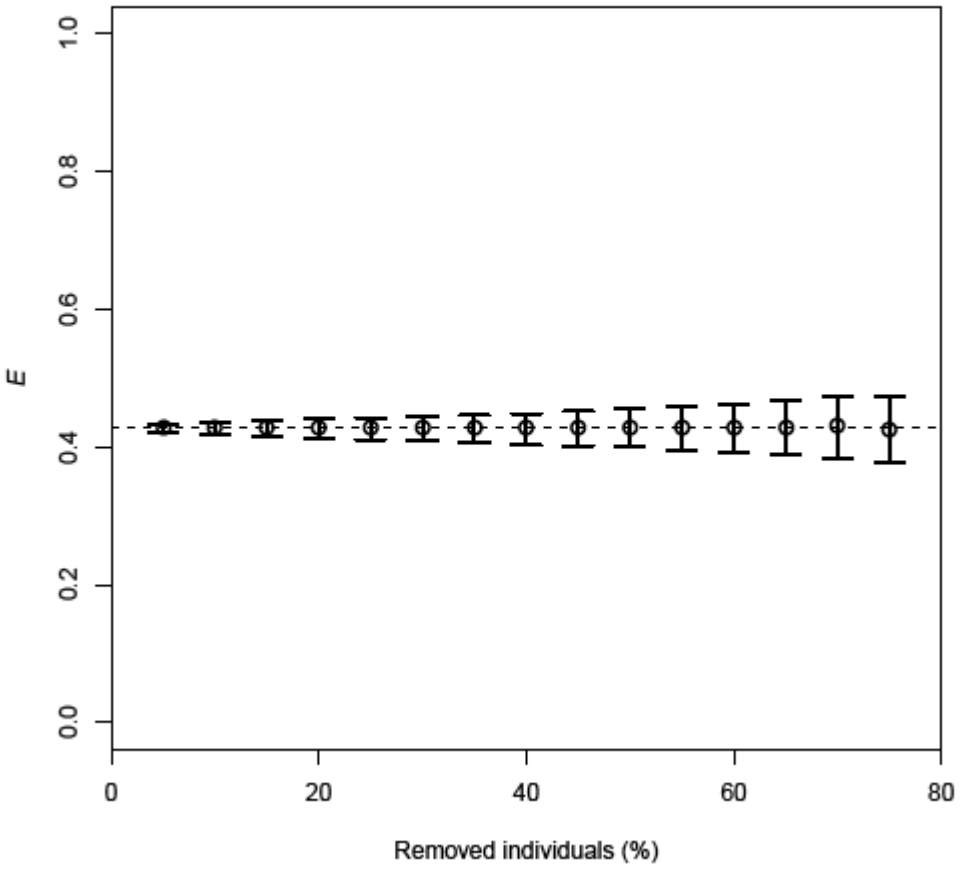
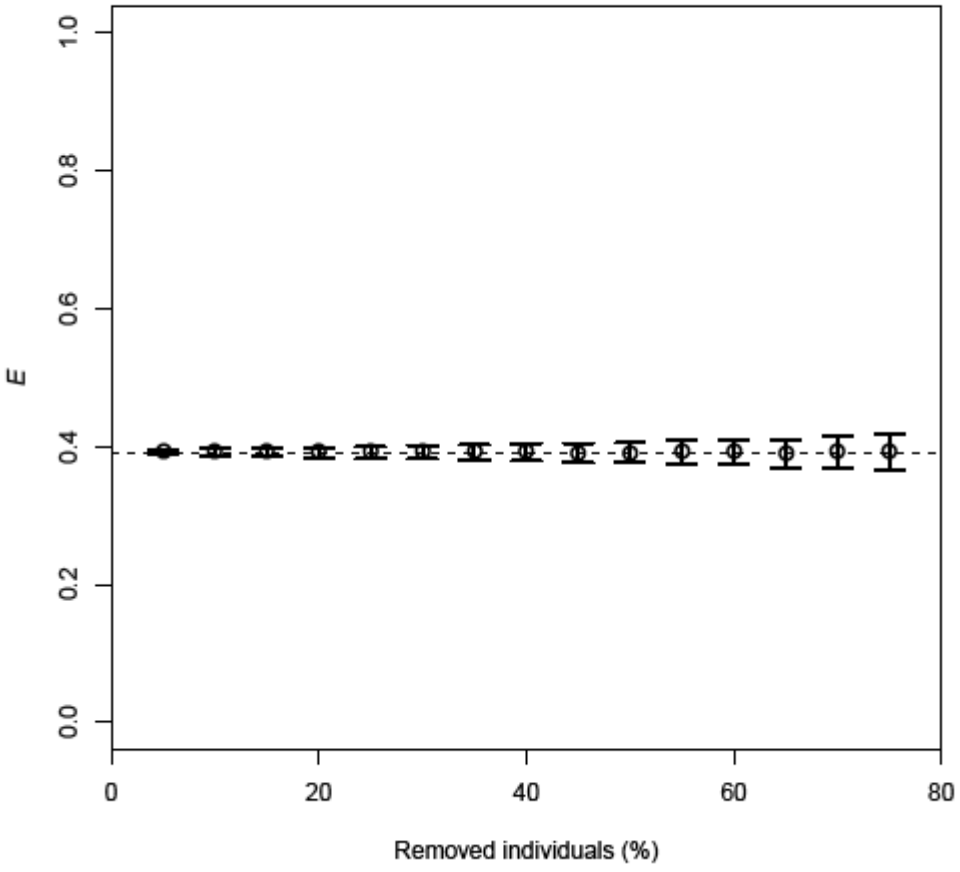
Fig. S1. Rarefaction of sampling effort for dietary data before and after the RHD outbreak and its effects on *E* (plot a: before; plot b: after), C_{ws} (plot c: before; plot d: after) and *NODF* (plot e: before; plot f: after). Note that *E*, C_{ws} and *NODF* values recorded for total sampling effort are within the confidence interval of *E*, C_{ws} and NODF values for rarefied matrices, suggesting that sample size did not affect our estimates. Circles represent means and bars standard deviation (n = 1,000 simulations for each fraction of total sampling effort).

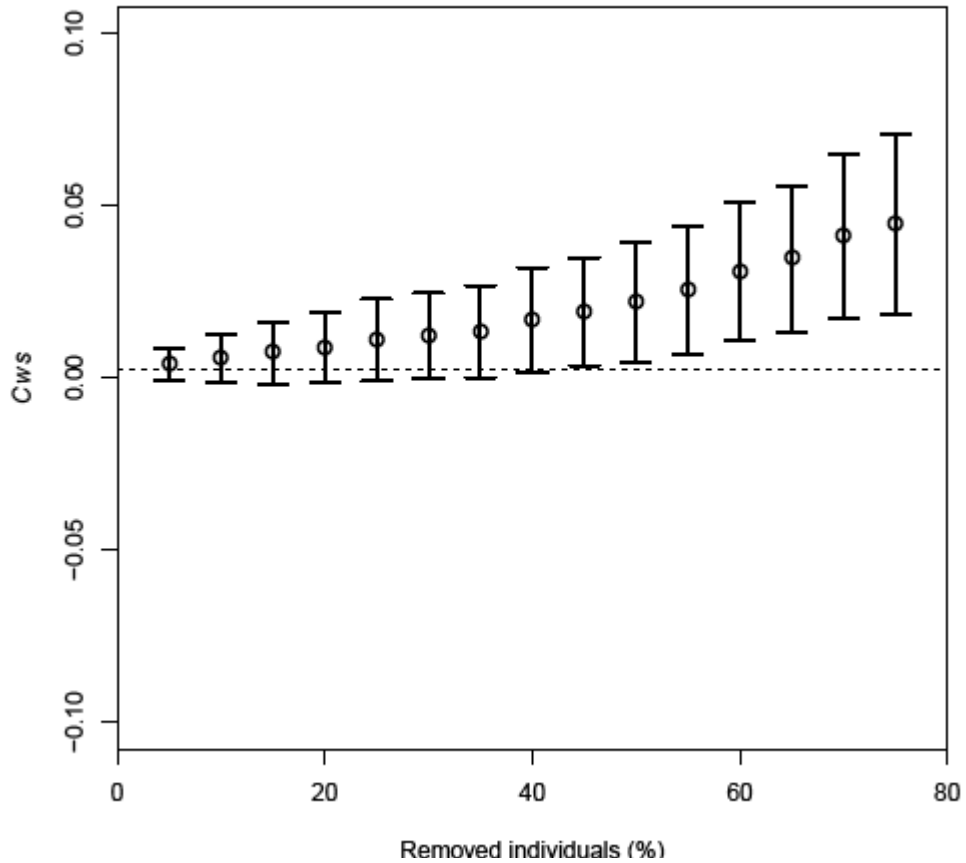
a


E
0.0
0.2
0.4
0.6
0.8
1.0
0
20
40
60
80
Removed individuals (%)

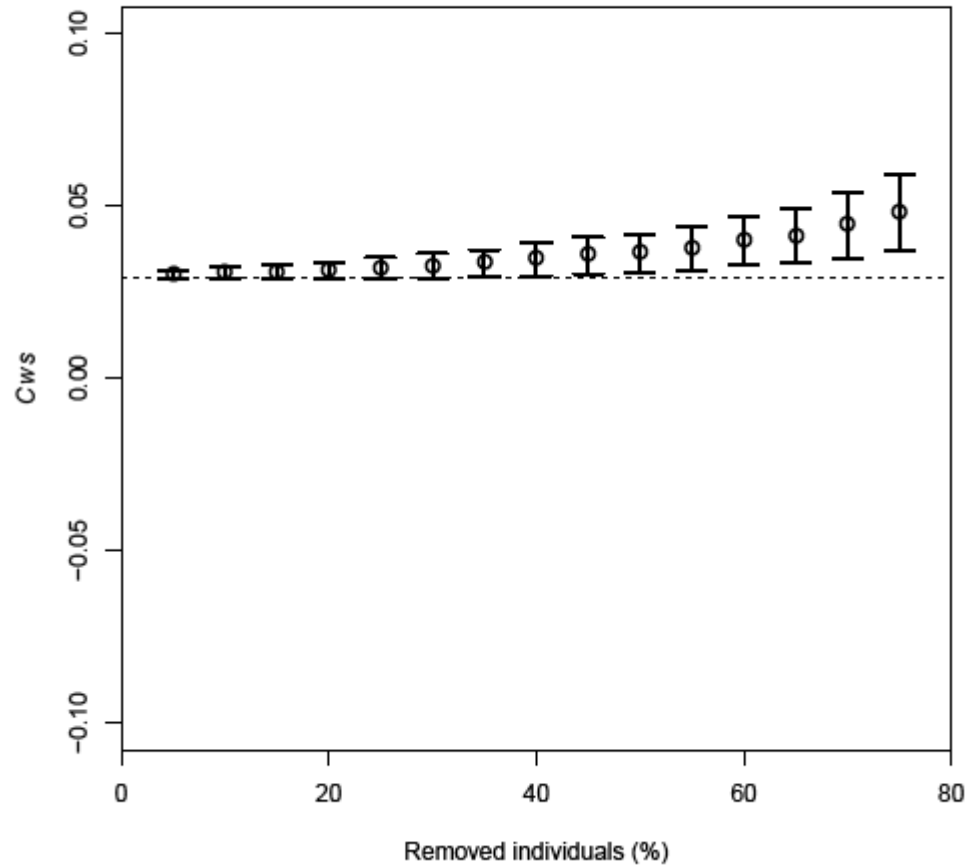
b


E
0.0
0.2
0.4
0.6
0.8
1.0
0
20
40
60
80
Removed individuals (%)

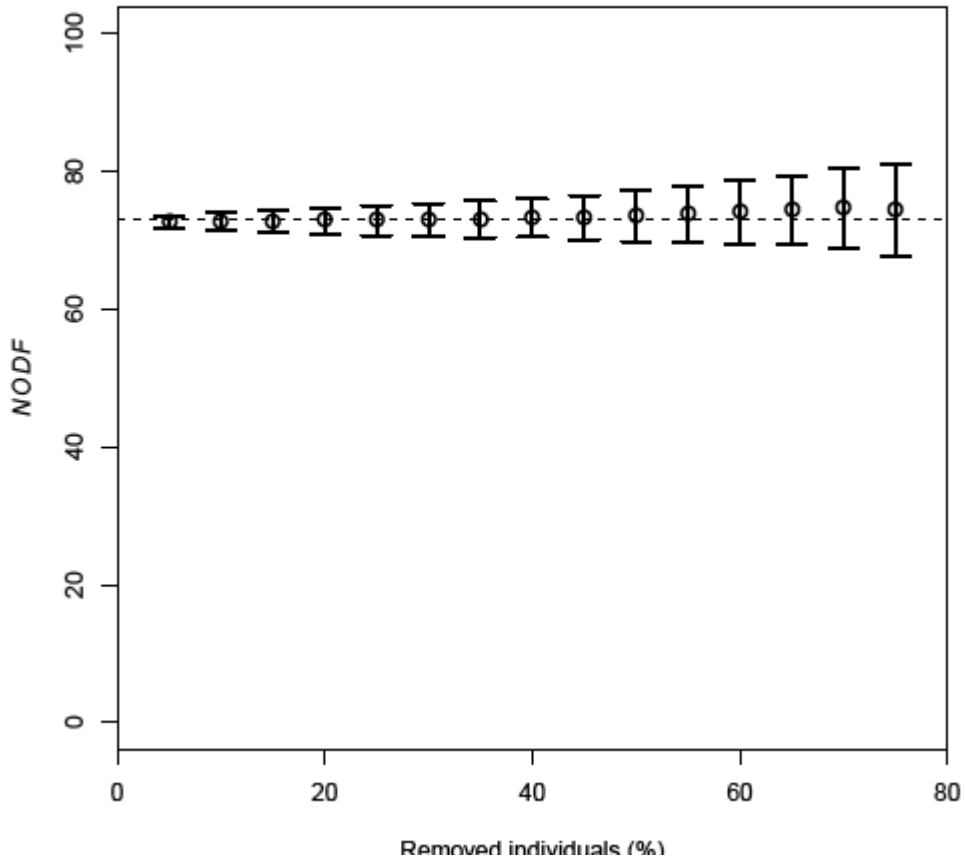
c


0.10
0.05
0.00
−0.05
−0.10
Cws
0
20
40
60
80
Removed individuals (%)

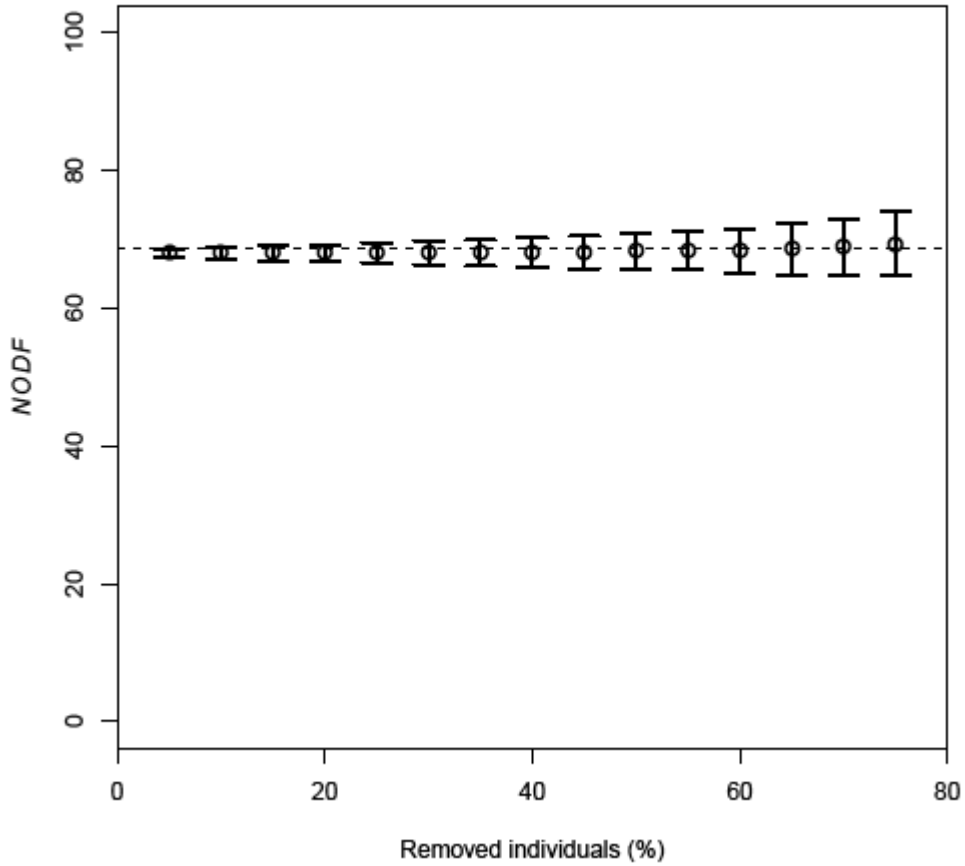
d


0.10
0.05
0.00
−0.05
−0.10
Cws
0
20
40
60
80
Removed individuals (%)

e


NODF
0
20
40
60
80
100
0
20
40
60
80
Removed individuals (%)

f


NODF
0
20
40
60
80
100
0
20
40
60
80
Removed individuals (%)