

How do vertebrates respond to mast seeding?

Michał Bogdziewicz, Rafał Zwolak and Elizabeth E. Crone

M. Bogdziewicz (http://orcid.org/0000-0002-6777-9034), (micbog@amu.edu.pl), and R. Zwolak, Dept of Systematic Zoology, Faculty of Biology, Adam Mickiewicz University, Umultowska 89, PL-61-614 Poznań, Poland. MB and E. E. Crone, Dept of Biology, Tufts University, 163 Packard Ave, Medford, MA 02155, USA. EEC also at: Harvard Forest, Harvard University, Petersham, MA 01366, USA.

Mast-seeding is the synchronized and intermittent production of a large seed crop by a population of plants. The cascading effects of masting on wildlife have been well documented in granivorous rodents. Yet, the effects of mast-seeding are potentially further reaching, since a number of generalist species can take advantage of mast years. We employed a full-text search algorithm to identify all papers that discussed effects of mast-seeding on wildlife, in addition to typical searches of titles and abstracts. We aimed to evaluate the breadth of wildlife species for which mast years are thought to be important drivers. In addition, we tested three hypotheses derived from past reviews: 1) species with lower reproductive potential (lower average litter size) are more likely to show aggregative responses to mast-seeding, 2) species with lower body sizes (lower mobility) are more likely to show reproductive responses, and 3) indirect consumers of mast (predators) are more likely to show aggregative responses than direct consumers. We found 186 articles including reports of response of 122 species of vertebrates to mast-seeding. Expectations were partly confirmed: relationships 1) and 2) held for mammals, but not for birds. However, 3) direct consumers were more likely than indirect consumers to show aggregative responses. Our tests of the first two hypotheses question the generality of past predictions for taxa other than mammals. Our test of the third hypothesis suggests that responses of direct and indirect consumers might depend on the type of resource pulse. Many of the examples in our analysis come from systems in which wildlife responses to mast have been less rigorously documented than the examples in past reviews. They suggest the range of wildlife responses to mast-seeding are more taxonomically and ecologically diverse than past reviews have widely recognized and point to directions for future research.

Resource pulses are large-magnitude, low frequency, and short duration events of increased resource availability (Yang et al. 2008). Pulsed productivity affects multiple ecosystem processes, including dynamics of populations, interactions between consumers and resources, top-down and bottom-up effects in food webs, and disease prevalence (Ostfeld and Keesing 2000, Yang et al. 2008). Mast seeding, defined as the intermittent production of a large seed crop by a population of plants (Kelly 1994, Crone and Rapp 2014), is a resource pulse of high magnitude and worldwide occurrence (Ostfeld and Keesing 2000, Yang et al. 2010). Examples of spectacular variation in seed production come from all continents except Antarctica (Kelly and Sork 2002, Espelta et al. 2008, Crone et al. 2009, Norghauer and Newbery 2010) and synchronization in pulse release may extend up to thousands of kilometers (Koenig and Knops 1998, 2000). A more limited set of studies have documented responses of wildlife populations to mast-seeding. These case studies provide examples of impacts of mast seeding that ramify throughout communities and cut across ecosystem boundaries (Jones et al. 1998, Curran and Leighton 2000, McShea 2000, Schmidt and Ostfeld 2003, 2008, Lobo and Millar 2013).

To date, most of these published examples of wildlife responses to mast-seeding show a similar taxonomic

structure: an increase of rodents (primary consumers) was followed by response of mustelids and raptors, and eventually caused a lagged increase in predation on birds' nests (King 1983, Jędrzejewska and Jędrzejewski 1998, McShea 2000, Clotfelter et al. 2007, Schmidt et al. 2008, Zwolak et al. 2015). The majority of wildlife population studies implicitly ignore effects of mast resource pulses, by using one or two years of data to generalize animal diets, demography and trophic relationships. One interpretation of this pattern is that mast-seeding mostly affects trophic chains that start with granivorous rodents. Alternatively, it may be that these case studies have been well developed and highly cited, but that similar cascading effects happen in other ecological systems. To the extent that wildlife population dynamics are generally driven by responses to pulsed resources, we need to change our perspective from one of relatively uniform conditions among years, to one of dynamic responses to a strongly fluctuating environment (Holt 2008, Yang et al. 2008).

In this article, we quantify the breadth and diversity of ways in which wildlife populations respond to mast-seeding, with the specific aim of capturing incidental observations of mast year effects, as well as deliberate experimental tests of how mast years affect wildlife. In order to capture these

observations, we developed a literature review approach that differs from a traditional meta-analysis. Specifically, we conducted a full-text search of entire articles in a selected subset of journals and identified all studies that mentioned masting anywhere in the text. The full-text search combined two sources of data: studies that were designed to test for effects of mast-seeding, and studies that attribute aspects of wildlife performance to mast events in a post hoc or incidental manner, even if masting was not originally part of the investigation. Thus, in one sense, the study is a much broader investigation than the traditional literature search, but this breadth comes at the cost of including qualitative observations, as well as explicit tests. We contrast the studies obtained with this full-text search algorithm to a conventional search that identified papers by keywords in titles and abstracts.

In addition to describing responses to mast-seeding, we use our data set of wildlife responses to mast-seeding to evaluate three hypotheses from two past reviews of consumer responses to pulsed resources. In the first of these reviews, Ostfeld and Keesing (2000) hypothesized that species responses to mast seeding should vary predictably as a function of the rate of population response (capacity to increase reproductive output, e.g. litter size) and species mobility (Table 1). In particular, species with slow life histories (“slow” sensu Stearns 1992) are more likely to respond to masting through mobility or a diet-switching (i.e. changes in the proportion of each prey species in the diet; Ostfeld and Keesing 2000) because of their low intrinsic capacity to increase reproductive output. Similarly, species with high reproductive capacity and poor mobility should respond via reproduction (Ostfeld and Keesing 2000). In the second review, Yang et al. (2010) found that the numerical increase in response to pulsed resources was larger for aggregative responses than reproductive ones. Aggregation was defined as a mechanism of numerical recruitment driven by the immigration of consumers from surrounding populations (Yang et al. 2010). Frequent occurrence of the aggregative or combined (aggregative and reproductive) response was hypothesized to be the cause of particularly strong numerical increases characterizing consumers from higher trophic levels (Yang et al. 2010).

We evaluate the three hypotheses outlined in the two previous reviews as follows: 1) to evaluate the hypothesis that aggregative or diet-switching responses are more likely to occur in species with slow life history and/or high mobility, we obtained data on average litter (or clutch) size and average body mass for species in our study. Litter size is tightly linked to life history (Millar and Zammuto 1983, Heppell

et al. 2000, Sæther and Bakke 2000) and has been used previously as an indicator of life history syndromes (Cardillo et al. 2003). Similarly, body mass has repeatedly been shown to correlate strongly with mobility in both birds and mammals, and has been successfully used as a surrogate of mobility in previous studies (Schoener 1968, Haskell et al. 2002, Carbone et al. 2005, Ottaviani et al. 2006, Thornton et al. 2011). We then tested whether the probability of aggregative and diet-switching responses is higher in species with lower average litter size and/or higher body mass. 2) To evaluate the hypothesis that reproductive response is more likely to occur in species with low mobility and/or fast life history, we tested whether the probability of species showing reproductive responses decreases with body mass and increases with litter size. 3) Finally, we compiled data on the trophic status of each species, in relation to mast seeding (granivore, consumer of granivores, etc). We tested whether indirect responses to masting, i.e. those at higher trophic levels, are more likely to be aggregative than reproductive.

Because of their irregular and unpredictable nature, effects of mast-seeding and other pulsed resources are inherently difficult to study. Our approach of finding and analyzing observations of wildlife responses to mast-seeding sheds new light on a relatively intractable phenomenon. Of course, the incidental observations are less rigorous evidence for how vertebrates respond to mast-seeding than the experimental tests. We see the analysis of these data as a valuable way to quantify our collective knowledge of natural history, and identify hypotheses that could be tested more rigorously.

Material and methods

Data base construction

We built two data bases, one using traditional literature search methods (hereafter traditional search or ‘TS’), and the other using full-text search. In the first, we searched ISI Web of Science and Scopus databases for peer-reviewed studies that examined the effects of mast seeding on wildlife using keyword search (*mast** AND *bird** OR *mammal** OR *rodent** OR *passer** OR *ungulat** OR *carniv** OR *animal** OR *wildlife** OR *ave** OR *omniv** OR *herbiv** OR *artiod** AND *acorn** OR *seed**). In the second, we downloaded all articles published in Ecology, Journal of Animal Ecology, Journal of Wildlife Management, Oikos, The Auk and Journal of Mammalogy between January 1990 (or January 1997 in the case of Ecology) and September 2013. The time range of articles downloaded from Ecology was narrower because volumes published before 1997 did not have pdf-files available to download from ESA website. Next, we screened all downloaded articles for the term ‘mast*’ appearing anywhere in the text. The search was done using the freeware application PDF-XChange Viewer ver. 2.5. We chose this set of ~20 000 articles as representative of ecologists studying wildlife from ecological and conservation/management perspectives. We read articles that included the *mast** term and divided them into studies designed to investigate the effects of mast seeding (hereafter targeted

Table 1. Predictions derived from Ostfeld and Keesing (2000) review article describing how probability of vertebrate responses to mast seeding should vary predictably with their reproductive output (here, litter size) and mobility (here, body mass). All relationships held, but only for mammals, not for birds. See main text for details.

Predictor: \ Response:	Aggregation and/or diet switching	Increase in reproductive output
Species average litter/clutch size	negative relationship	positive relationship
Species average body mass	positive relationship	negative relationship

studies: ‘FT’ studies, for ‘full text, targeted’) and studies where effects of masting were found incidentally (hereafter non-targeted studies: ‘NT’ studies). We categorized studies with predictions on the effects of masting in the introduction section and studies where research design explicitly incorporated masting as FT studies. We categorized articles in which potential mast effects were mentioned in discussion as a possible explanation of results as NT studies. In general, NT studies were articles in which authors attributed wildlife responses to mast seeding without formal statistical analysis (e.g. high survival in a given year explained by observed background mast seeding). Based on information contained in article, we scored the type of species response (see list of responses in Results) to masting. We divided these responses into three broad categories (behavioral, demographic and physiological responses).

For each study, we recorded the identity of the masting plant species, the identity of all wildlife species that responded, and whether the response was a direct or an indirect effect of masting. Direct effects included those that were directly caused by increased availability of seeds for their primary consumers and the indirect effects included those that were caused by changes in populations of primary consumers in response to mast seeding (Ostfeld and Keesing 2000). For each wildlife species, we also recorded its body mass and mean litter size. The average body masses were obtained from Project PanTHERIA, a global species-level data set of life history ecological traits (Smith et al. 2003, Lislevand et al. 2007, Jones et al. 2009). Information on the species average litter size was obtained from AnAge Database of Animal Ageing and Longevity (Tacutu et al. 2013). Data on a few species that were not available in the above mentioned databases were obtained from other peer-reviewed sources.

Statistical analysis

We tested predictions derived from Ostfeld and Keesing (2000) and Yang et al. 2010 using generalized linear mixed effects models (GLMMs) implemented via ‘lme4’ package (Bates et al. 2013), with taxonomic order of each species as a random effect. We tested the first prediction (species with lower reproductive capacity or higher mobility are more likely to respond through aggregation or diet switching) by building two models: in the first, we modeled the probability of reporting diet switching or aggregative response as the function of average litter size, and an interaction of litter size with species class (mammals versus birds). In the second, we replaced litter size with log-transformed body mass. We tested the second prediction (species with low mobility or high reproductive capacity are more likely to show a reproductive response) using two models with reproductive response as a binary (yes/no) response variable. In the first one, we used log-transformed average body mass and the interaction of body mass with species class as explanatory variables. In the second, we replaced body mass with litter size.

We tested whether primary and secondary consumers of mast differ in the mechanism of their responses to mast with two analyses. In the first, we modeled the probability of aggregative response in relation to trophic distance; in the

second, we evaluated how trophic distance influences the probability of reproductive response.

In all models we used species as the unit of replication. In other words, if at least one study reported a type of response (e.g. reproduction) for a species, that response was included as present in that species, and if a species was included in our data base but no studies had reported that type of response, that response type was scored as absent. In all models we added the number of articles reporting response of focal species as covariate to control for differences in numbers of reports on particular species. Moreover, in all above-described models we tested whether the results of hypotheses testing would differ across different search methods. To do this, in first four models (testing the hypotheses from Ostfeld and Keesing 2000) we used three-way interaction term (life history trait \times species class \times type of search method used to found evidence of species response), and in the next two models (testing the hypothesis from Yang et al. 2010) two-way interaction term (trophic distance \times search method).

We tested whether distribution of species taxonomic orders, prevalence of behavioral, demographic and physiological responses, and frequency of direct and indirect effects differed across articles found with different search methods (traditional search, targeted and non-targeted studies from alternative search) using multinomial logistic regression implemented via the ‘nnet’ package (Venables and Ripley 2002). All statistics were computed in R (<www.r.project.org>).

Results

The nature of the dataset

Our two databases included 186 articles: 67 obtained with the traditional search and 138 with the full-text search, of which 19 overlapped between data bases (Supplementary material Appendix 1 Table A1). These studies generated 426 data points (response by species combinations). Full-text search generated 298 data points: 207 assigned to the FT category (studies designed to investigate the effects of masting, 86 articles) and 91 to the NT category (effect of mast seeding that were found incidentally, 52 articles). The sum of FT and NT articles exceeds 119 because some articles that were set up to test particular mast-related hypothesis also reported incidental findings (Noyce and Garshelis 1997, Clark et al. 2005, Jensen et al. 2012).

The majority of studies reported responses to mast-seeding of deciduous trees, mainly oaks (47% of studies, e.g. *Quercus rubra*, *Q. crispula*, *Q. serrata*, *Q. falcata*), and beech (22% of studies, *Fagus grandifolia*, *F. sylvatica*, *Nothofagus* spp.). Other deciduous species (26%) included *Acer* spp., *Carya* spp., *Castanea* spp., *Dipterocarpaceae* spp., *Fraxinus* spp. Thirteen percent of studies recorded masting effects of coniferous species (e.g. *Abies lasiocarpa*, *Juniperus* spp., *Pinus abies*, *Pinus albicaulis*, *Pinus edulis*, *Picea glauca*). Three studies included responses to bamboo masting and one to masting of *Chionochloa* grass (Wilson and Lee 2010).

Overall, 55 species of mammals and 67 species of birds, belonging to 14 orders and 42 families, were reported to respond to masting (Supplementary material Appendix 1

Table A1). Rodents were most often reported to respond to mast seeding (50% of TS articles, 44% of FT and 42% of NT articles; Supplementary material Appendix 1 Fig. A2), followed by carnivores (TS: 14%, FT: 20%, NT: 23%), Passeriformes (TS: 14%, FT: 15%, NT: 3%), Artiodactyla (TS: 6%, FT: 11%, NT: 11%) and Galliformes (TS: 5%, FT: 2%, NT: 18%). Responses of the remaining taxonomic orders (Accipitriformes, Anseriformes, Columbiformes, Piciformes, Psittaciformes, Strigiformes, Primates, Scandentia and Soricomorpha) were found in less than 5% of all reports (Supplementary material Appendix 1 Fig. A1). The distribution of taxonomic orders differed across search methods ($\chi^2 = 22.83$, DF = 8, $p = 0.004$). Taxa had similar prevalence in TS and FT articles ($\chi^2 = 3.87$, DF = 8, $p = 0.86$). However, the distribution of taxa in NT articles differed from the distribution in FT articles ($\chi^2 = 18.13$, DF = 8, $p = 0.02$), and marginally from TS articles ($\chi^2 = 13.46$, DF = 8, $p = 0.09$). Based on inspection of 95% confidence limits, this difference was driven by four significant differences among four taxonomic groups: rodents were over-represented in TS studies, passerines were under-represented in NT studies, Galliformes were over-represented in NT studies, and carnivores were more common in NT than in TS studies.

Types of responses to masting

Studies in our database reported a diversity of responses by wildlife to mast seeding (Supplementary material Appendix 1 Table A1). Demographic responses (reproduction, survival, nest success) were most often reported (TS: 28%, FT: 31%, NT: 23%; Supplementary material Appendix 1 Fig. A2), followed by changes in species abundance (TS: 32%, FT: 23%, NT: 17%). Behavioral responses to masting included changes in movement patterns (TS: 11%, FT: 13%, NT: 20%), habitat selection (TS: 1%, FT: 9%, NT: 9%), and diet (TS: 15%, FT: 8%, NT: 11%). Physiological changes induced by masting included body condition, torpor and hibernation time (TS: 8%, FT: 12%, NT: 9%). The distribution of responses did not differ between search methods ($\chi^2 = 4.44$, DF = 4, $p = 0.34$).

In addition to effects of mast seeding, we found numerous reports of consequences of mast failure (TS: 2 articles, FT: 14, NT: 6) on focal organisms. Mast failure was attributed to cause a variety of wildlife responses in categories resembling those reported for mast seeding: reproduction, survival, nest success, abundance, immigration, body condition, diet-switching, changes in daily distance moved, and capture probability.

Hypothesis 1. Are species with lower reproductive capacity (slower life histories) more likely to respond through aggregation or diet switching?

As predicted by Ostfeld and Keesing (2000), we found a negative relationship between litter size and probability of recording aggregative or diet switching response (Fig. 1). However, this relationship held only for mammals ($z = -2.66$, $p = 0.007$), and not for birds ($z = -0.82$, $p = 0.39$). Similarly, the probability of aggregative and diet switching responses was positively related to body mass in mammals ($z = 4.41$, $p > 0.001$; Fig. 2), but not in birds ($z = -0.07$, $p = 0.94$).

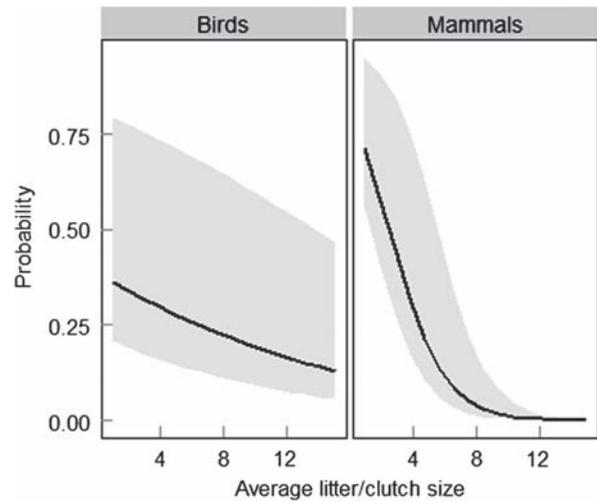


Figure 1. Generalized linear mixed model curves representing the average marginal probability of displaying aggregative or diet switching response in relation to clutch (birds) and litter (mammals) size to mast seeding. Shaded regions represent confidence intervals (95%) for the curve.

Reproductive response was more likely to be recorded for mammals than birds (20 mammal species, and 9 bird species with reproductive response recorded; $z = 2.20$, $p = 0.027$). The relationship between litter size and aggregative responses differed marginally with search methods ($\chi^2 = 5.22$, DF = 2, $p = 0.07$, but this effect was driven by the different magnitude of the effect size of mammals' response, which was larger in TS than NT studies (litter size effect in NT: -2.14 intercept ± 0.88 SE, TS: -0.54 ± 0.24); the direction of the relationship stayed the same. In case of body mass and aggregative/diet switching response the relationship did not differ with search methods ($\chi^2 = 1.09$, DF = 2, $p = 0.58$).

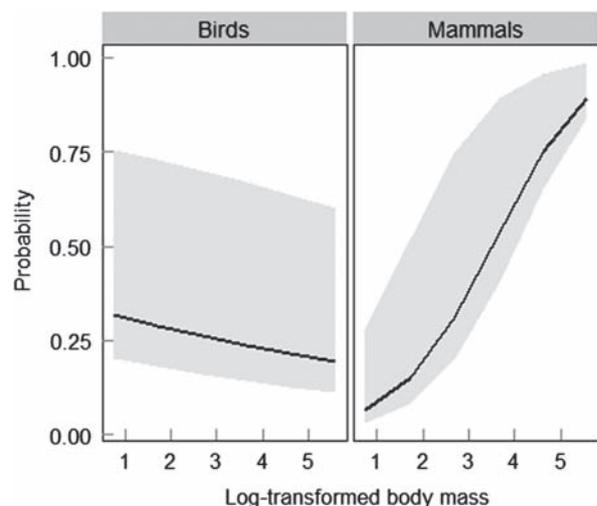


Figure 2. Generalized linear mixed model curves representing the average marginal probability of displaying aggregative or diet switching response in relation to log-transformed body mass to masting. Shaded regions represent confidence intervals (95%) for the curve.

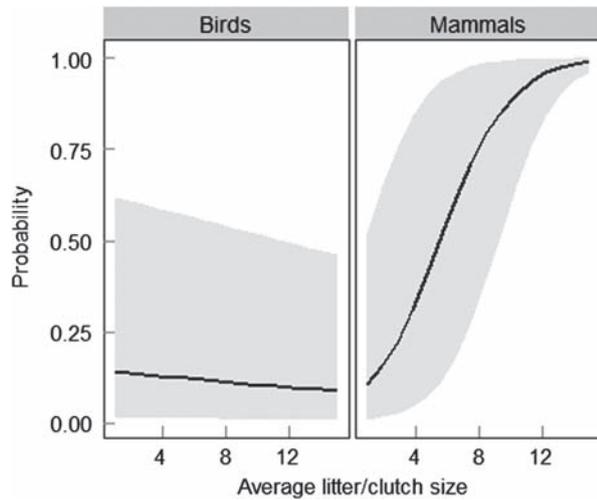


Figure 3. Generalized linear mixed model curves representing the average marginal probability of displaying reproductive response in relation to clutch (birds) and litter (mammals) size to mast seeding. Shaded regions represent confidence intervals (95%) for the curve.

Hypothesis 2. Are smaller (less mobile) species more likely to show reproductive response?

As predicted by Ostfeld and Keesing (2000), we found a negative relationship between body size and the probability of recording species increase in reproductive investment in response to mast seeding, although this response was not statistically significant at the $p < 0.05$ level. This relationship was stronger for mammals ($z = -1.73$, $p = 0.08$; Fig. 3), than for birds ($z = 1.40$, $p = 0.16$). Moreover, in case of birds, the non-significant relationship between body size and reproductive response was positive. The probability of recording reproductive response was positively related to litter size in mammals ($z = 3.31$, $p > 0.001$; Fig. 4), but not in birds ($z = -0.27$, $p = 0.78$). Aggregation and diet switching was equally likely to be recorded for mammals and birds (26 mammal, 22 bird species with focal response; $z = 0.82$, $p = 0.41$). The outcome of hypothesis testing did not

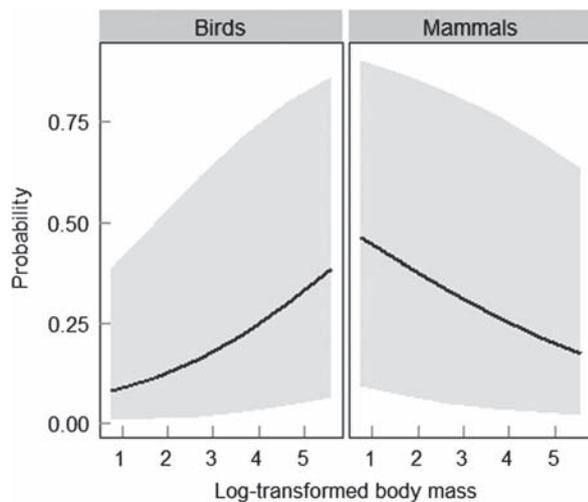


Figure 4. Generalized linear mixed model curves representing the average marginal probability of displaying reproductive response in relation to log-transformed body mass to masting. Shaded regions represent confidence intervals (95%) for the curve.

differ across search methods (test with body mass: $\chi^2 = 0.99$, $DF = 2$, $p = 0.61$; test with litter size: $\chi^2 = 0.06$, $DF = 2$, $p = 0.97$).

Hypothesis 3. Are indirect consumers more likely to respond to mast seeding through aggregation?

Contrary to expectations, aggregative response was more likely to be associated with direct than indirect consumers ($z = 2.22$, $p = 0.026$). The probability of reproductive responses did not differ between direct and indirect consumers ($z = 0.68$, $p = 0.49$). The outcome did not differ across search methods (aggregative response: $\chi^2 = 0.01$, $DF = 2$, $p = 0.99$; reproduction: $\chi^2 = 1.19$, $DF = 2$, $p = 0.55$). Generally, aggregative responses were recorded for 23 species and reproductive responses for 29 species. Only five species were recorded to respond jointly by these two mechanisms: the bearded pig *Sus barbatus*, the black bear *Ursus americanus*, crested partridge *Rollulus rouloul*, the great tit *Parus major* and the jungle fowl *Lophura* spp.

Discussion

Overall, we found reports of response to mast seeding for 122 species of vertebrates belonging to 14 orders and 43 families. In the studies identified through the full-text literature search, responses to mast were not strongly biased toward granivorous rodents and their food webs. In fact, many species respond to masting, including passerines, large omnivores such as bears, ungulates and primates, and generalist birds such as mallards and pheasants (Supplementary material Appendix 1). Moreover, the diversity of responses shown by passerines expanded beyond nest success and resembled those reported for rodents, making these two groups equally responsive to mast seeding.

High reproductive capacity and low mobility are tightly linked with reproductive response in mammals, but not in birds. In small mammals with high reproductive capacity (e.g. rodents), mast seeding effects on reproductive output are well-appreciated and described: masting increases the number of juveniles per female (Bergeron et al. 2011), increases proportion of yearling and adult breeders (Boutin et al. 2006), induces winter breeding (Pucek et al. 1993), and has long-lasting positive effects on reproductive success of females born in mast year (Descamps et al. 2008). In contrast, masting effects on reproductive ecology of birds are much less known and are rarely the focus of research. The best described effects on birds' recruitment are indirect via a mast-rodent-predators-nest success link: i.e. changes in nest predation (McShea 2000, Schmidt and Ostfeld 2008), and brood size of birds of prey (Jędrzejewski et al. 1996). Our literature review shows that birds also respond directly to mast-seeding. For example, clutch size tends to be higher in mast years in Galliformes (Curran and Leighton 2000, Devers et al. 2007). In addition, in great tits mast failure decreases recruitment (Grøtan et al. 2009), and influences fledging production (Bouwhuis et al. 2010). Overall, increase in abundance is the most often reported response to mast seeding for both birds and mammals. These studies of reproductive responses in birds did not show up in the traditional literature search because 'mast' was not among

the key words. Thus, we suggest that more explicit studies of the role of mast seeding for birds' reproductive ecology would be a useful area for future research.

The lack of association between body size and the aggregative response/diet switching in birds might be the result of overall higher mobility of birds than mammals, which may allow them to move freely among habitats (Fraser and Stutchbury 2004, Thornton et al. 2011). Indeed, among mammals, large-scale movement in response to mast was reported for bears and ungulates, while, among birds, movement between habitats was reported for species as large as turkeys (average body mass 7400 g) and as small as red-breasted nuthatches (11 g). In contrast to aggregative responses, diet switching involved a much higher diversity of mammal species, indicating that potential for large-scale movement between habitats drove the relationship between body size and diet switching. The potential for movement in relation to mast-seeding could be incorporated into conservation plans of large mammals. For example, attraction to mast can move focal species outside protection areas and decrease their survival (Beringer et al. 1998). It can also induce predictable fluctuations in herbivore pressure across landscapes as large mammals such as ungulates, aggregate in mast-rich areas.

In their review, Yang et al. (2010) found that indirect responses to resource pulses tend to be larger in magnitude than direct ones. They suggested that a higher likelihood of aggregative or combined response in indirect consumers might be responsible for this pattern, since these two mechanisms created the most powerful increases. We found only five species with such a combined response to mast seeding. Moreover, contrary to the expectation, the likelihood of aggregative response was higher in direct than in indirect consumers. This pattern was mostly driven by generalist birds that aggregate in mast-rich habitats (Koenig 2001, Koenig and Knops 2001, Sæther et al. 2007). Yang et al. (2010) included only one example of changes in bird abundance, thus the difference in results might be related to different taxa included in its and our analyses. Alternatively, our findings might imply that wildlife responses to mast seeding differ from responses to pulsed resources in general.

Our full-text search pointed wildlife responses that are often attributed to mast seeding, but have to date rarely been the focus of research. For example, many NT studies attribute changes in habitat selection to mast seeding. Mechanisms include both aggregation toward mast-resources, and indirect responses to changes in population density. Few targeted studies (TS) have explored how mast-seeding changes habitat selection (but see e.g. Kilpatrick et al. 2011). Therefore, researchers interested in habitat selection should be particularly aware that the selected habitats are likely to vary through time. Importantly, ignoring mast effects could lead to false interpretation of results: e.g. habitat could be wrongly assigned as a sink while the low survival in population is caused by mast failure (Mahon and Martin 2006).

We also found a variety of effects of mast failure on wildlife. Such a variety of phenomena explained by mast failure suggest that events of resource scarcity may have similarly broad effects on ecosystems as mast itself; especially in ecosystems where some seed production usually happens, e.g. in North American hardwood forests (McShea 2000, Kelly et al. 2008). We speculate that, in systems where abundant

resources are common, occasional resource troughs could contribute to population and community dynamics, with equally far-reaching effects to resource pulses. However, the theoretical implications of famine pulses in food webs have been largely overlooked (but see Sears et al. 2004). Thus, it is unclear if they act simply as mast years à rebours or whether they have their own, unique effects.

One limitation of our review is that it is biased towards temperate hardwood forests. This was not intended, but is logical in hindsight based on the set of journals that we chose for full-text search. Inclusion of journals specializing in tropical or Southern Hemisphere would be an interesting direction for future research. We suspect that the bias towards hardwood forests reflects researcher bias, as this pattern was evident in both search methods, rather than lack of important mast–consumer interactions in conifer-dominated or grassland systems (Wilson and Lee 2010, Lobo and Millar 2013, Lobo 2014).

In conclusion, many aspects of animal ecology may be influenced by highly dynamic processes such as mast-seeding. Ecologists have long been aware of the importance of “rare” or “surprising” events (Weatherhead 1986, Doak et al. 2008, Lindenmayer et al. 2010), but these are inherently difficult to study. Our full-text approach to identify examples of responses to mast-seeding is broadly analogous to other ‘big data’ studies in ecology, in which we obtain low-resolution data over broad scales in space and time (Dickinson et al. 2012, Breed et al. 2013, Szymkowiak and Kuczyński 2015). As our data-processing abilities increase, and journal access increases, this approach may be a valuable way to broaden our understanding of the importance of different kinds of rare events in general.

Acknowledgements – We would like to thank Agnieszka Amborska for her invaluable help with screening articles. The work was done while RZ and MB were supported by a (Polish) National Science Centre Harmonia grant no. 2012/04/M/NZ8/00674 awarded to RZ. MB was supported by Adam Mickiewicz Univ. Foundation Scholarship awarded in 2014 and by National Science Centre grant ‘Etiuda’ no. 2015/16/T/NZ8/00018 for preparation of doctoral dissertation. EEC was supported by NSF DEB 10-20889 and funding from Harvard Forest.

References

- Bates, D. et al. 2013. lme4: linear mixed-effects models using Eigen and S4. – R package ver. 1.0-4.
- Bergeron, P. et al. 2011. Anticipation and tracking of pulsed resources drive population dynamics in eastern chipmunks. – *Ecology* 92: 2027–2034.
- Beringer, J. et al. 1998. The influence of a small sanctuary on survival rates of black bears in North Carolina. – *J. Wildl. Manage.* 62: 727–734.
- Boutin, S. et al. 2006. Anticipatory reproduction and population growth in seed predators. – *Science* 314: 1928–1930.
- Bouwhuys, S. et al. 2010. Individual variation in rates of senescence: natal origin effects and disposable soma in a wild bird population. – *J. Anim. Ecol.* 79: 1251–1261.
- Breed, G. A. et al. 2013. Climate-driven changes in northeastern US butterfly communities. – *Nat. Clim. Change* 3: 142–145.
- Carbone, C. et al. 2005. How far do animals go? Determinants of day range in mammals. – *Am. Nat.* 165: 290–297.

- Cardillo, M. et al. 2003. Geographic range size, life history and rates of diversification in Australian mammals. – *J. Evol. Biol.* 16: 282–288.
- Clark, J. D. et al. 2005. Bait stations, hard mast, and black bear population growth in Great Smoky Mountains National Park. – *J. Wildl. Manage.* 69: 1633–1640.
- Clofelter, E. D. et al. 2007. Acorn mast drives long-term dynamics of rodent and songbird populations. – *Oecologia* 154: 493–503.
- Crone, E. E. and Rapp, J. M. 2014. Resource depletion, pollen coupling, and the ecology of mast seeding. – *Ann. N. Y. Acad. Sci.* 1322: 21–34.
- Crone, E. E. et al. 2009. How do plants know when other plants are flowering? Resource depletion, pollen limitation and mast-seeding in a perennial wildflower. – *Ecol. Lett.* 12: 1119–1126.
- Curran, L. and Leighton, M. 2000. Vertebrate responses to spatiotemporal variation in seed production of mast-fruiting Dipterocarpaceae. – *Ecol. Monogr.* 70: 101–128.
- Descamps, S. et al. 2008. Cohort effects in red squirrels: the influence of density, food abundance and temperature on future survival and reproductive success. – *J. Anim. Ecol.* 77: 305–314.
- Devers, P. K. et al. 2007. Ruffed grouse population ecology in the Appalachian region. – *Wildl. Monogr.* 168: 1–36.
- Dickinson, J. L. et al. 2012. The current state of citizen science as a tool for ecological research and public engagement. – *Front. Ecol. Environ.* 10: 291–297.
- Doak, D. F. et al. 2008. Understanding and predicting ecological dynamics: are major surprises inevitable? – *Ecology* 84: 952–961.
- Espelta, J. M. et al. 2008. Masting mediated by summer drought reduces acorn predation in Mediterranean oak forests. – *Ecology* 89: 805–817.
- Fraser, G. S. and Stutchbury, B. J. 2004. Area-sensitive forest birds move extensively among forest patches. – *Biol. Conserv.* 118: 377–387.
- Grøtan, V. et al. 2009. Spatial and temporal variation in the relative contribution of density dependence, climate variation and migration to fluctuations in the size of great tit populations. – *J. Anim. Ecol.* 78: 447–459.
- Haskell, J. P. et al. 2002. Fractal geometry predicts varying body size scaling relationships for mammal and bird home ranges. – *Nature* 418: 527–530.
- Heppell, S. S. et al. 2000. Life histories and elasticity patterns: perturbation analysis for species with minimal demographic data. – *Ecology* 81: 654–665.
- Holt, R. D. 2008. Theoretical perspectives on resource pulses. – *Ecology* 89: 671–681.
- Jensen, P. G. et al. 2012. Marten and fisher responses to fluctuations in prey populations and mast crops in the northern hardwood forest. – *J. Wildl. Manage.* 76: 489–502.
- Jędrzejewska, B. and Jędrzejewski, W. 1998. Predation in vertebrate communities: the Białowieża Primeval Forest as a case study. – Springer.
- Jędrzejewski, W. et al. 1996. Tawny owl (*Strix aluco*) predation in a pristine deciduous forest (Białowieża National Park, Poland). – *J. Anim. Ecol.* 65: 105–120.
- Jones, C. G. et al. 1998. Chain reactions linking acorns to gypsy moth outbreaks and Lyme disease risk. – *Science* 279: 1023–1026.
- Jones, K. E. et al. 2009. PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals: Ecological Archives E090–184. – *Ecology* 90: 2648–2648.
- Kelly, D. 1994. The evolutionary ecology of mast seeding. – *Trends Ecol. Evol.* 9: 465–470.
- Kelly, D. and Sork, V. L. 2002. Mast seeding in perennial plants: why, how, where? – *Annu. Rev. Ecol. Syst.* 33: 427–447.
- Kelly, D. et al. 2008. An intercontinental comparison of the dynamic behavior of mast seeding communities. – *Popul. Ecol.* 50: 329–342.
- Kilpatrick, H. J. et al. 2011. Effects of landscape and land-ownership patterns on deer movements in a suburban community. – *Wildl. Soc. B.* 35: 227–234.
- Koenig, W. D. 2001. Spatial autocorrelation and local disappearances in wintering North American birds. – *Ecology* 82: 2636–2644.
- Koenig, W. D. and Knops, J. M. 1998. Scale of mast-seeding and tree-ring growth. – *Nature* 396: 225–226.
- Koenig, W. D. and Knops, J. M. 2000. Patterns of annual seed production by northern hemisphere trees: a global perspective. – *Am. Nat.* 155: 59–69.
- Koenig, W. D. and Knops, J. M. 2001. Seed-crop size and eruptions of North American boreal seed-eating birds. – *J. Anim. Ecol.* 70: 609–620.
- King, C. M. 1983. The relationships between beech (*Nothofagus* Sp.) seedfall and populations of mice (*Mus musculus*), and the demographic and dietary responses of stoats (*Mustela erminea*), in three New Zealand forests. – *J. Anim. Ecol.* 52: 141–166.
- Lindenmayer, D. B. et al. 2010. Improved probability of detection of ecological “surprises”. – *Proc. Natl. Acad. Sci. USA* 107: 21957–21962.
- Lislevand, T. et al. 2007. Avian body sizes in relation to fecundity, mating system, display behavior and resource sharing. – *Ecology* 88: 1605.
- Lobo, N. 2014. Conifer seed predation by terrestrial small mammals: a review of the patterns, implications, and limitations of top-down and bottom-up interactions. – *For. Ecol. Manage.* 328: 45–54.
- Lobo, N. and Millar, J. S. 2013. Indirect and mitigated effects of pulsed resources on the population dynamics of a northern rodent. – *J. Anim. Ecol.* 82: 814–825.
- Mahon, C. L. and Martin, K. 2006. Nest survival of chickadees in managed forests: habitat, predator and year effects. – *J. Wildl. Manage.* 70: 1257–1265.
- McShea, W. J. 2000. The influence of acorn crops on annual variation in rodent and bird populations. – *Ecology* 81: 228–238.
- Millar, J. S. and Zammuto, R. M. 1983. Life histories of mammals: an analysis of life tables. – *Ecology* 64: 631–635.
- Norghauer, J. M. and Newbery, D. M. 2010. Recruitment limitation after mast-seeding in two African rain forest trees. – *Ecology* 91: 2303–2312.
- Noyce, K. V. and Garshelis, D. L. 1997. Influence of natural food abundance on black bear harvests in Minnesota. – *J. Wildl. Manage.* 61: 1067–1074.
- Ostfeld, R. S. and Keesing, F. 2000. Pulsed resources and community dynamics of consumers in terrestrial ecosystems. – *Trends Ecol. Evol.* 15: 232–237.
- Ottaviani, D. et al. 2006. Body mass as a predictive variable of home-range size among Italian mammals and birds. – *J. Zool.* 269: 317–330.
- Pucek, Z. et al. 1993. Rodent population dynamics in a primeval deciduous forest (Białowieża National Park) in relation to weather, seed crop, and predation. – *Acta Theriol.* 38: 199–232.
- Schmidt, K. A. and Ostfeld, R. S. 2003. Songbird populations in fluctuating environments: predator responses to pulsed resources. – *Ecology* 84: 406–415.
- Schmidt, K. A. and Ostfeld, R. S. 2008. Numerical and behavioral effects within a pulse-driven system: consequences for shared prey. – *Ecology* 89: 635–646.
- Schmidt, K. A. et al. 2008. Wood thrush nest success and post-fledging survival across a temporal pulse of small mammal abundance in an oak forest. – *J. Anim. Ecol.* 77: 830–837.
- Schoener, T. W. 1968. Sizes of feeding territories among birds. – *Ecology* 49: 123–141.

- Sears, A. L. W. et al. 2004. Feast and famine in food webs: the effects of pulsed productivity. – In: Polis, G. A. et al. (eds), *Food webs at the landscape level*. Chicago Univ. Press, pp. 359–386.
- Sæther, B.-E. and Bakke, Ø. 2000. Avian life history variation and contribution of demographic traits to the population growth rate. – *Ecology* 81: 642–653.
- Sæther, B.-E. et al. 2007. The extended Moran effect and large-scale synchronous fluctuations in the size of great tit and blue tit populations. – *J. Anim. Ecol.* 76: 315–325.
- Smith, F. A. et al. 2003. Body mass of late Quaternary mammals. – *Ecology* 84: 3403.
- Stearns, S. C. 1992. *The evolution of life histories*. – Oxford Univ. Press.
- Szymkowiak, J. and Kuczyński, L. 2015. Avoiding predators in a fluctuating environment: responses of the wood warbler to pulsed resources. – *Behav. Ecol.* doi:10.1093/beheco/aru237.
- Tacutu, R. et al. 2013. Human Ageing Genomic Resources: integrated databases and tools for the biology and genetics of ageing. – *Nucleic Acids Res.* 41: D1027–D1033.
- Thornton, D. H. et al. 2011. The influence of landscape, patch, and within-patch factors on species presence and abundance: a review of focal patch studies. – *Landscape Ecol.* 26: 7–18.
- Venables, W. N. and Ripley, B. D. 2002. *Modern applied statistics with S*, 4th edn. – Springer.
- Weatherhead, P. J. 1986. How unusual are unusual events? – *Am. Nat.* 128: 150–154.
- Wilson, D. J. and Lee, W. G. 2010. Primary and secondary resource pulses in an alpine ecosystem: snow tussock grass (*Chionochloa* spp.) flowering and house mouse (*Mus musculus*) populations in New Zealand. – *Wildl. Res.* 37: 89–103.
- Yang, L. H. et al. 2008. What can we learn from resource pulses. – *Ecology* 89: 621–634.
- Yang, L. H. et al. 2010. A meta-analysis of resource pulse–consumer interactions. – *Ecol. Monogr.* 80: 125–151.
- Zwolak, R. et al. 2015. Beech masting modifies the response of rodents to forest management. – *For. Ecol. Manage.* doi: 10.1016/j.foreco.2015.10.017.

Supplementary material (available online as Appendix oik.03012 at <www.oikosjournal.org/readers/appendix>). Appendix 1.