

# Extreme environmental variation sharpens selection that drives the evolution of a mutualism

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The importance of infrequent events for both adaptive evolution and the evolution of species interactions is largely unknown. We investigated how the infrequent production of large seed crops (masting) of a bird-dispersed tree (whitebark pine, *Pinus albicaulis*) influenced phenotypic selection exerted by its primary avian seed predator–disperser, the Clark’s nutcracker (*Nucifraga columbiana*). Selection was not evident during common years of low seed abundance, whereas it was replicated among areas and favoured traits facilitating seed dispersal during infrequent years of high seed abundance. Since nutcrackers act mostly as seed predators during small seed crops but as seed dispersers during the largest seed crops, trees experienced strong selection from nutcrackers only during infrequent years when the interaction was most strongly mutualistic. Infrequent events can thus be essential to both adaptive evolution and the evolutionary dynamics of species interactions.

**Keywords:** adaptive evolution; environmental variation; mutualism; phenotypic selection; seed/predation dispersal

## 1. INTRODUCTION

Despite the importance of natural selection in nature, we have little knowledge of whether most adaptive evolutionary change is a result of organisms responding to selection in more common environmental conditions or in less frequent conditions (Nathan 2006). Our knowledge is limited because only a few studies have documented the consequences of infrequent environmental conditions for temporal variation in selection and evolutionary change (e.g. Merilä *et al.* 2001 and references therein; Grant & Grant 2002; Reimchen & Nosil 2002). We have even less knowledge of how environmental variation affects both the strength of selection and the form of species interactions, yet species interactions are recognized as a prominent source of selection driving adaptive evolution (Thompson 2005). For example, environmental variation can affect the form of an interaction (i.e. whether it is mutualistic or antagonistic) and thus potentially alters the direction of selection (Thompson & Cunningham 2002; Nuismer *et al.* 2003; Thompson & Fernandez 2006). However, the long-term evolutionary consequences of such variation in the wild are unknown. We address these issues by examining how a widespread source of variation in environmental conditions affects selection and the consequences of such varying selection for the evolution of a seed dispersal mutualism.

Seed masting, the large inter-annual variation in seed crop sizes within a population, is taxonomically and geographically widespread and is a spectacular example of temporal variation in environmental conditions for seed consumers and plant recruitment (Janzen 1976; Herrera *et al.* 1998; Kelly & Sork 2002). Differences

between mast and non-mast years in seed abundance can exceed several orders of magnitude (Jansen *et al.* 2004). Potential benefits to plants from masting include satiating seed predators, enhancing pollination and facilitating seed dispersal (Janzen 1976; Herrera *et al.* 1998; Kelly & Sork 2002; Vander Wall 2002; Jansen *et al.* 2004), with cascading effects occurring throughout the ecosystems (Ostfeld & Keesing 2000). Plant traits that influence seed dispersal should be under strong selection because successful seed dispersal can enhance plant fitness by reducing distance- or density-dependent seed predation, lowering intraspecific competition and placing seeds at sites suitable for germination (Willson & Traveset 2001). While masting in some animal-dispersed plants enhances plant fitness by increasing the likelihood of successful seed dispersal (Vander Wall 2002; Jansen *et al.* 2004), the extent to which masting affects patterns of selection by seed dispersers on traits related to seed dispersal is largely unknown (Jansen *et al.* 2004). Similarly, we lack evidence for how the variable seed pulse caused by masting affects the form of interactions between seed dispersers and plants. More generally, masting provides an exceptional opportunity to investigate how variable environmental conditions (i.e. mast years) influence patterns of selection and the evolution of species interactions.

Nutcrackers (*Nucifraga*) are the primary seed dispersers of several large-seeded (greater than 90 mg) pines (*Pinus*) in North America and Eurasia, including whitebark pine (*Pinus albicaulis*; Tomback & Linhart 1990; Lanner 1996; Tomback *et al.* 2001a). The seed dispersal mutualism between nutcrackers and pines is regarded as a ‘keystone mutualism’ because it is critical for the establishment of unique terrestrial ecosystems (Lanner 1996; Tomback *et al.* 2001a). Whitebark pine, like many masting plants, produce large seed crops in 1 year, followed by

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years of low or no seed production. During large cone-production years, an individual nutcracker can harvest and cache roughly 3–5 times the number of seeds actually eaten (Vander Wall & Balda 1977; Tomback 1982). The surplus caching of seeds during large cone crops leaves many available to germinate, such that trees with traits that result in a greater number of seeds harvested over the lifetime of the tree should gain a fitness advantage (Siepielski & Benkman 2007, in press).

We conducted field studies to quantify phenotypic selection by Clark's nutcrackers (*Nucifraga columbiana*) on cone and seed traits of whitebark pine across several different populations displaying a range of size variation in cone crops. This approach allowed us to investigate how selection varied in response to variation in cone production typically exhibited within a single population over a much broader time-scale (figure 1a). We then investigate how the form of the interaction (i.e. whether mutualistic or antagonistic) between nutcrackers and whitebark pine varied in response to resource (seed) abundance. We find that temporal variation in seed abundance is a critical factor underlying the evolution of the seed dispersal mutualism between nutcrackers and pines, and that it may also be a general feature governing the adaptive evolution of plant reproductive traits via their interactions with seed predators.

## 2. MATERIAL AND METHODS

### (a) *Whitebark pine cone abundance*

During each of 26 years, the Interagency Grizzly Bear Study Team counted the number of cones on 56–209 trees (mean = 156 trees) along 19 transects in Yellowstone National Park, Wyoming. Values are presented as the mean number of cones per tree averaged across all transects within a year. These values encompass the range of variation we detected among our study populations (figure 1) and thus provide a long-term perspective on variation in cone crop sizes.

### (b) *Patterns of phenotypic selection on cone and seed traits by nutcrackers*

We assumed that potential differences in selection among populations producing different cone crop sizes represent the kinds of differences in selection within any one population over a range of cone crop sizes. Given the range of variation in cone production found among sites over 2 years is comparable to that over 26 years at another site (figure 1), this appears to be a reasonable assumption. We also note that cone crop sizes vary from year to year in each population (Siepielski & Benkman 2007), with all populations producing both small and large cone crops.

We used regression analyses (Lande & Arnold 1983) to estimate the targets and form of selection exerted by nutcrackers on cone and seed traits of whitebark pine. Whitebark pine is dependent on Clark's nutcrackers for seed dispersal (Tomback 1982; Lanner 1996), as seeds not harvested by nutcrackers are generally not dispersed and most of these seeds remain in cones where they become inviable (Lanner 1996). To make inferences about selection and the evolutionary consequences of selection, it is important to use a measure of fitness that reflects lifetime fitness. For short-lived, annual plants, it is appropriate to use the number of seeds harvested, but for long-lived plants, such as whitebark pine that live to be 1000 or more

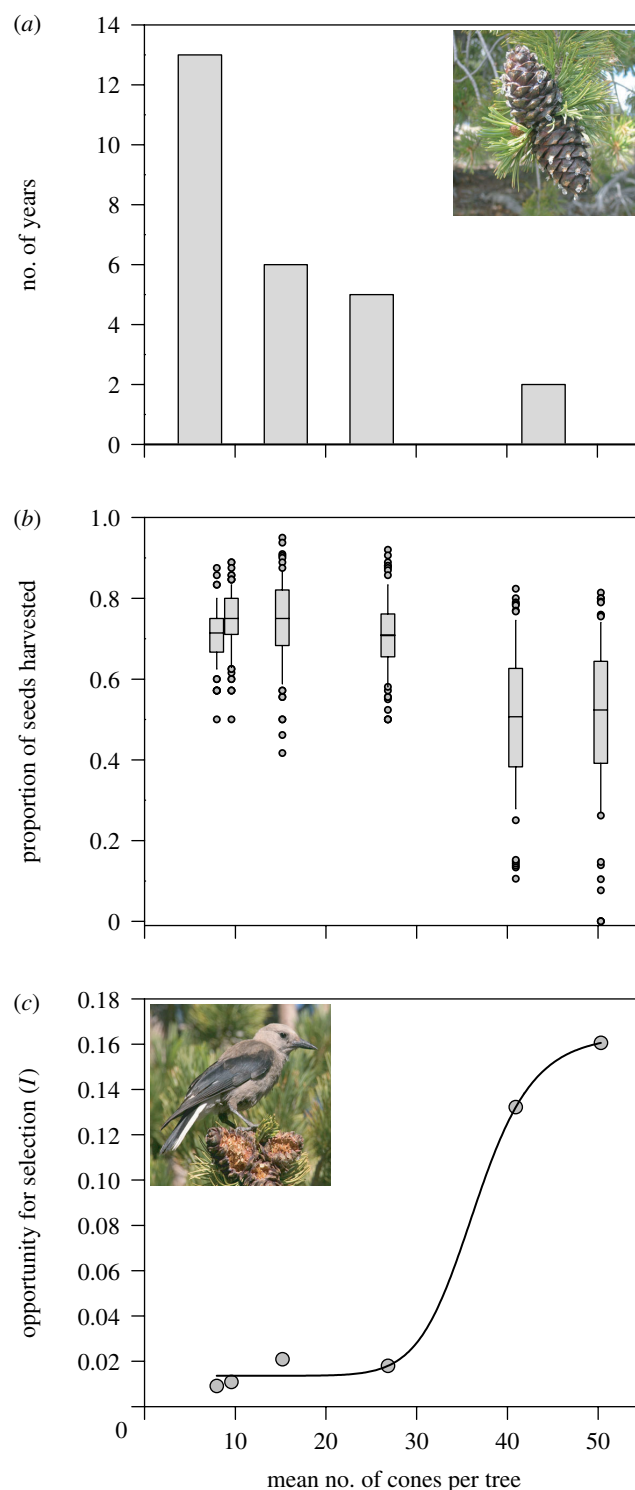


Figure 1. Annual variation in whitebark pine cone abundance, its relationship to seed removal and the opportunity for selection by Clark's nutcrackers. (a) The frequency distribution of cone crops ( $n=26$  years). (b) Variation in the proportion of seeds harvested by nutcrackers among six populations producing different cone crop sizes. Line within boxes (box plots) indicates median, lower and upper boundaries of the box indicate 25th and 75th percentiles, and error bars indicate 10th and 90th percentiles, respectively. Study sites from left to right are as follows: East Humboldt Range, Ruby Mountains, Independence Mountains, Jarbidge Mountains 2005, Pine Forest Range and Jarbidge Mountains 2004. (c) The opportunity for selection in the six populations in (b) increases when more cones are produced (nonlinear four-parameter logistic regression model:  $F_{3,5}=193.70$ ,  $r^2=0.99$ ,  $p=0.005$ ).

years old (Perkins & Swetnam 1996), this measure may inaccurately reflect lifetime fitness when selection is measured during only a small fraction of the tree's lifespan. Using the number of seeds harvested as a measure of fitness potentially confounds variation in cone (seed) production among individuals owing to variation in age (the number of cones produced by a whitebark pine increases with size/age; Weaver & Forcella 1986), which varied among trees at our study sites, with selection on cone traits arising from foraging preferences of nutcrackers. For example, if a tree produced cones with traits that nutcrackers preferred and thus consistently harvested all of their seeds, it would always be assigned a high fitness regardless of its age if we used percent of seeds harvested, whereas its assigned fitness would largely depend on its size/age relative to other trees when the study was conducted if we used total number of seeds harvested. Thus, we used the proportion of seeds harvested by nutcrackers as a surrogate for tree fitness (Jordano 1995) in the context of selection by nutcrackers. Although the proportion of seeds may be a better surrogate of fitness for an extremely long-lived iteroparous species whose reproductive output is size (and age) dependent, we note that our estimates of selection coefficients may not be directly comparable to studies that are able to measure lifetime fitness. One assumption is that cone traits do not change in a consistent manner as trees age. We have no reason to suspect such variation, nor did we find that nutcracker tree preferences varied with the number of cones produced at sites where selection was detected ( $r_s \leq 0.18$ ,  $p \geq 0.10$  for correlations between number of cones on tree and proportion of seed harvested by nutcrackers; table 1 in the electronic supplementary material). Nevertheless, we also summarize the results of the analyses using the total number of seeds harvested when they differ from those using the proportion of seeds harvested.

During mid-September 2005, we recorded both the number of cones that had signs of nutcracker seed-harvesting activity (shredded cones on trees; figure 1c) and the total number of cones on each tree for at least 78 trees at each of five mountain ranges in the Great Basin (Siepielski & Benkman 2007; table 1 in the electronic supplementary material). The proportion of seeds harvested was calculated as the number of cones with seeds harvested divided by the total number of cones on the tree. We also include data for the Jarbidge Mountains during 2004 (Siepielski & Benkman 2007). This is the only study site for which we have a multiple-year comparison and inclusion of this study site allows us to more explicitly make inter-annual comparisons. Since the proportion of seeds harvested by nutcrackers increases with time (Hutchins & Lanner 1982), we minimized the potential that our sampling method would bias the proportion of seeds harvested to be greater in populations with low cone abundance by estimating seed removal at populations with low cone abundance first and high cone abundance last. All 2005 populations were visited during the same 2 weeks of the year.

We measured the following cone and seed traits: closed cone length, maximum width of closed cone, cone mass with seeds removed, peduncle diameter, thickness of six scales from the middle portion of the distal third and the proximal third of the cone (scales were selected approx. equidistant around the cone and were measured near their distal end), number of scales crossed by a transect along the central axis of the cone, distance from the distal end of the

scale to the seed, number of empty and full seeds, and for five seeds from each cone we measured kernel masses, seed coat masses and seed coat thicknesses (seed coat thickness was measured at the flattest surface of the seed coat). The ratio of total seed mass to cone mass was calculated as the number of full seeds multiplied by the mean mass of an individual seed divided by cone mass. All length measurements were made to the nearest 0.01 mm with digital callipers. All mass measurements were made to the nearest 0.1 mg with a digital scale after cones and seeds were oven-dried at 60–70°C for more than 2 days. Mean trait values per tree were used in analyses, standardized to zero mean and unit variance, and individual tree fitness was converted into relative fitness by dividing individual tree fitness by mean population fitness. Tests of significance for regression coefficients were based on 1000 bootstrap replicates using the paired regression technique (Efron & Tibshirani 1993).

### (c) *The opportunity for selection*

The opportunity for selection ( $I$ ) is the variance in relative fitness and describes the upper bound of the intensity of selection that can act on a trait (Crow 1958; Arnold & Wade 1984).  $I$  was calculated for each population separately as  $\sum(\text{relative fitness} - \text{mean relative fitness})^2/n$ , where  $n$  is the sample size. We used a nonlinear four-parameter logistic regression model to examine the relationship between mean cone crop size and  $I$ .

### (d) *Abundances of nutcrackers and full seeds*

We used 10 min, 50 m fixed-radius point counts to estimate nutcracker abundance where selection was estimated. Within each mountain range where selection was measured, we established five point count locations at 500 m intervals along each transect in mature whitebark pine stands. Point counts were conducted between 06.00 and 11.00 from mid-August to early September during both 2004 and 2005. We assumed that detection probabilities did not differ in a consistent manner between populations, owing to the overall similarity of study areas and that only a single observer (A.M.S.) conducted the counts.

We used the point-quarter method (Mueller-Dombois & Ellenberg 1974) to estimate stand density of cone-bearing whitebark pine. Along a single transect at 10 locations spaced approximately every 500 m, we recorded the distance to the nearest cone-bearing tree in each of the four quadrants. We estimated seed abundance per tree at each study population by counting the number of cones present on the 10 nearest trees at each point count location using binoculars and multiplying this value by the population mean number of full seeds per cone (Siepielski & Benkman 2007). Seed density (full seeds per hectare) was calculated by multiplying the estimated seed abundance per tree by tree density. We used mean nutcracker abundance and mean seed density estimates combined over all point counts within a study area to provide one estimate for each parameter per year. A linear regression of the form  $y = a + bx^{-1}$  was used to examine the relationship between nutcracker abundance per full seed per hectare in relation to the number of full seeds per hectare. Since regressions where the dependent variable is a ratio composed of the independent variable may be prone to spurious correlations, we used bootstrapping (as above) to assess significance (Brett 2004).



### 3. RESULTS AND DISCUSSION

Our results indicate that nutcrackers exert selection on cone and seed traits only when cone crops are large (figure 2; table 1 in the electronic supplementary material). For example, directional selection (both direct (multiple regressions) and indirect (pairwise regressions) selection) favoured trees with more full seeds per cone and thinner proximal scales, and was replicated in areas with large cone crops (figure 2a; table 1 and figure 1 in the electronic supplementary material). Selection also consistently favoured trees with seeds that had thinner seed coats. Moreover, the selection exerted by nutcrackers was also replicated in another bird-dispersed pine, limber pine (*Pinus flexilis*), during large cone crops (Siepielski & Benkman 2007, *in press*). We focus our discussion on two traits (proximal scale thickness and the number of full seeds per cone) because they were the targets of selection (see multiple regressions in table 1 in the electronic supplementary material) and we have a good understanding of the functional significance of these traits as they relate to seed harvest by nutcrackers. In Siepielski & Benkman (2007, *in press*), we discuss patterns of selection on other traits. Why nutcrackers exert selection and why nutcrackers and trees benefit from such selection is relatively straightforward. Nutcrackers benefit by harvesting a greater proportion of seeds from trees that reward them with more energy per unit time, with trees concomitantly benefiting by having proportionately more of their seeds harvested and potentially germinating (Siepielski & Benkman 2007, *in press*). For example, selection favouring trees that produce cones with more seeds and thinner scales (figure 2a) allows nutcrackers to more quickly harvest seeds so that more seeds can be cached benefiting both nutcrackers and trees (Siepielski & Benkman 2007, *in press*).

In contrast, we detected no evidence of selection when small cone crops (fewer than 30 cones per tree) were produced (figure 2b). Particularly striking is the comparison between the Jarbidge Mountains in 2004 and 2005. Selection was strong during the large cone crop in 2004 (figure 2a), but absent in 2005 when the cone crop was only about half as large (figure 2b). The lack of selection during small cone crops presumably occurred because there was little variation in the proportion of seeds harvested among trees (figure 1b) regardless of the amount of variation in measured cone and seed traits (figure 2; table 1 in the electronic supplementary material). This accounts for the sharp decline in the opportunity for selection as mean cone abundance decreased (figure 1c). Previous studies also suggested that selection by nutcrackers is potentially weak because they remove seeds from all cones (Tomback & Linhart 1990). Our data support this contention, but only when cone crops are small (figure 1b). When these analyses were performed using the number of seeds harvested as a measure of tree fitness, the only target of selection was the number of full seeds per cone, and we detected selection during all sizes of cone crops. However, consistent with the other analyses using the proportion of seeds harvested, the selection gradients for each cone trait during the two largest cone crops were on average 5.6 times larger (range = 0–17.5) than those during the four small cone crops.

Alternatively, the absence of selection in populations with small cone crops could arise if only a subset of individuals produced cones leading to less phenotypic

variation within populations. However, this explanation is not supported by regressions among sites between the coefficient of variation of a given trait and cone crop size, which were usually non-significant and variable in direction (table 2 in the electronic supplementary material). The simplest explanation is that large cone crops probably saturate the harvesting abilities of nutcrackers, preventing them from removing many seeds from at least some trees (i.e. those trees whose seeds are least accessible to nutcrackers; figure 2a), whereas during small cone crops, nutcrackers rapidly harvest most seeds (figure 1b). This is supported by Scheffe's tests, which confirm that all populations producing fewer than 30 cones per tree had a significantly higher proportion of seeds harvested than populations producing more than 30 cones per tree (figure 1b;  $p < 0.05$  for all comparisons) while populations within the two categories did not differ from each other (figure 1b;  $p > 0.05$  for all comparisons). Assuming the long-term dataset of whitebark pine cone crops (figure 1a) is representative of most populations, selection by nutcrackers would probably have occurred only twice in 26 years (number of times mean number of cones exceeded 30). With a generation time of between 80 and 100 years (Krawoski 2001), whitebark pine will experience about seven episodes of strong selection per generation.

Matings also has consequences for the form of the interaction between nutcrackers and pines because cone crop size influences the number of seeds dispersed and cached (benefits) relative to the number of seeds eaten (costs; Janzen 1976; Vander Wall & Balda 1977). Nutcrackers probably become increasingly antagonistic to the pines as the number of birds per seed increases (figure 3) because proportionately more seeds are consumed before caching and nutcrackers probably recover and consume proportionately more of the seeds they cache. For example, when pinyon pine (*Pinus edulis*) produced few cones, its avian seed disperser, the pinyon jay (*Gymnorhinus cyanocephalus*), ate most of the seeds and cached few, if any of them (Ligon 1978). Similarly, seed-dispersing rodents recovered proportionately more cached pine seeds when few seeds were produced than when many seeds were produced (Vander Wall 2002). This implies that nutcrackers probably shifted from being mutualists to antagonists with whitebark pine, as seed abundance decreased because the number of nutcrackers per seed increased (figure 3). Not surprisingly, therefore, most (greater than 14 times more) whitebark pine seedling recruitment occurs following large seed crops (Tomback *et al.* 2001b) when the number of nutcrackers per seed is lowest (figure 3).

Even though nutcrackers were probably antagonistic to whitebark pine during the more common years of low seed abundance, potential seed defences directed at nutcrackers were unlikely to evolve because nutcrackers did not exert selection at this time (figure 2b). If we used the number of seeds harvested instead of the proportion of seed harvested as a measure of fitness, the tree preferences exhibited by nutcrackers may not have translated into differential reproduction for the trees (and thus selection exerted by nutcrackers) because very little recruitment occurred during this time (e.g. Tomback *et al.* 2001b). Rather, selection occurred only when large seed crops were produced (figure 2a), so that the net effect should be for cone and seed traits to experience selection when the interaction is most strongly mutualistic. This predicted

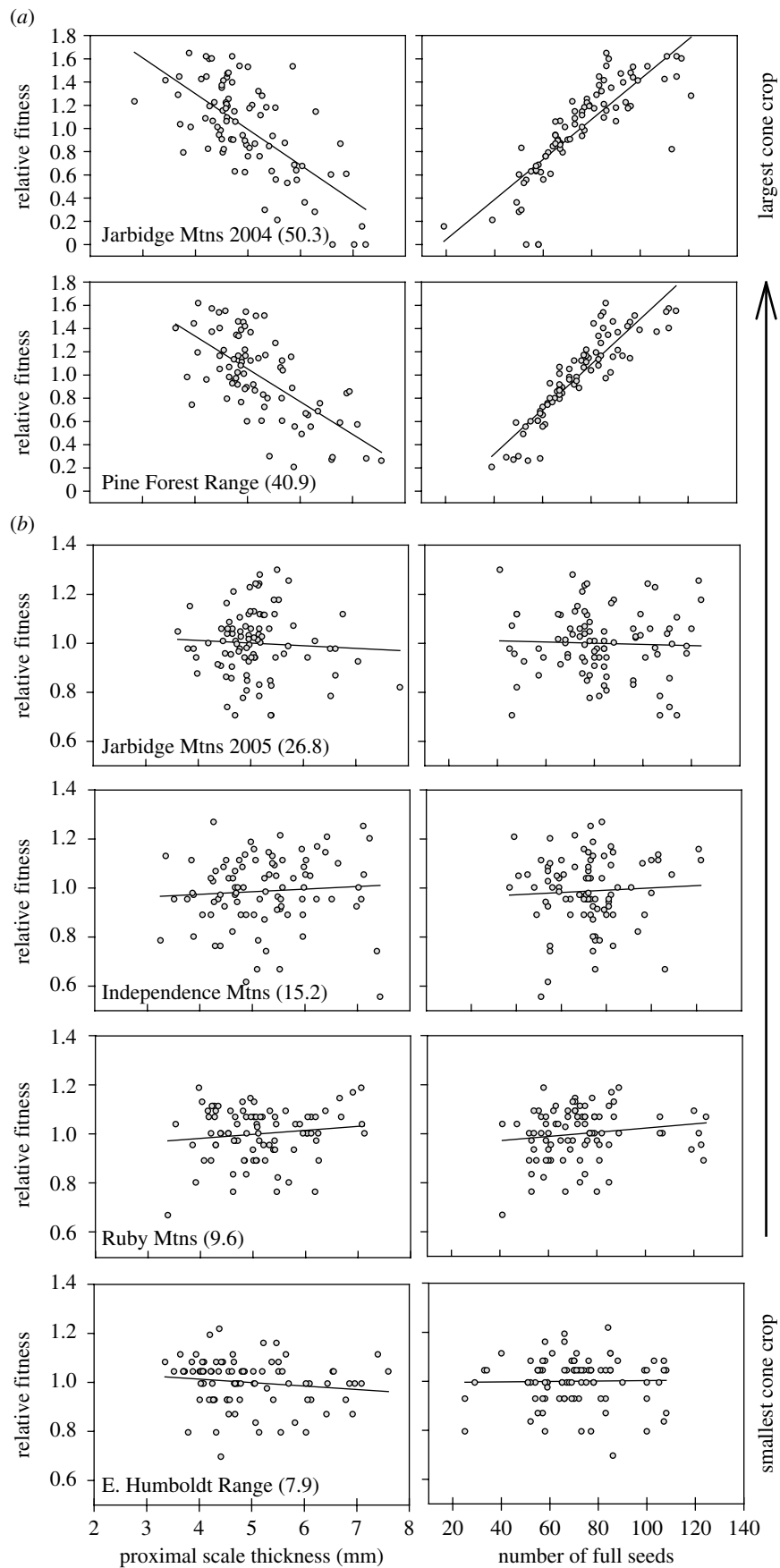


Figure 2. Phenotypic selection by Clark's nutcrackers on whitebark pine cone traits is evident and replicated only when large cone crops are produced. Plots show how relative tree fitness varies in relation to proximal cone scale thickness (left column) and the number of full (containing female gametophyte) seeds per cone (right column) for (a) large (selection evident and replicated) and (b) decreasingly smaller (selection not evident) cone crops (mean number of cones per tree). We detected evidence for selection only when cone crop sizes were more than 30 cones per tree (table 1 in the electronic supplementary material).

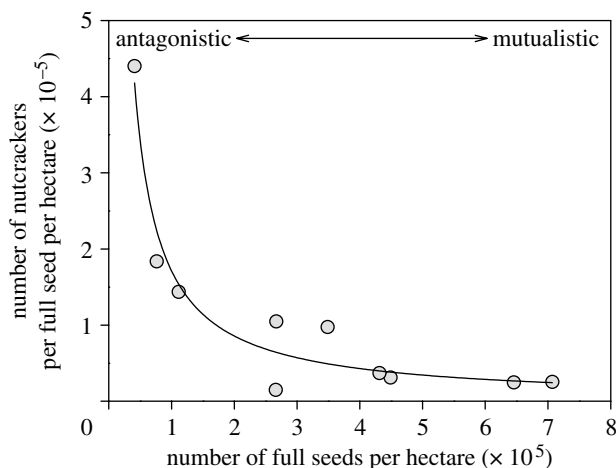


Figure 3. The mean number of Clark's nutcrackers per full whitebark pine seed per unit area decreases with increases in the mean number of full seeds per unit area. The implication is that nutcrackers consequently shift from being antagonistic to increasingly mutualistic with the pine because they eat proportionately fewer of the seeds they cache. The curve is a linear regression of the form: mean nutcrackers per full seed per hectare =  $2.96(\times 10^{-8}) + 1.65(\text{mean number of full seeds per hectare})^{-1}$  ( $F_{1,8} = 130.06$ ,  $p < 0.0001$ ,  $r^2 = 0.94$ ; bootstrapped test of the slope:  $t = 4.38$ ,  $p = 0.002$ ).

evolutionary effect was found by comparing cone structures between areas with and without an important pre-emptive seed competitor and seed predator, the pine squirrel (*Tamiasciurus* spp.), which was absent from areas in our study but elsewhere counters selection exerted by nutcrackers (Siepielski & Benkman 2007, in press). For instance, whitebark pine has more full seeds per cone and thinner proximal scales in areas without pine squirrels, as expected if selection by nutcrackers was an important factor driving the evolution of cone and seed traits (Siepielski & Benkman 2007, in press). Unlike other patterns of variation in selection attributed to environmental conditions, for example, oscillating selection in Darwin's finches (Grant & Grant 2002), the punctuated selection caused by masting results in selection occurring in only one direction, which may actually quicken the rate of adaptive evolution of traits facilitating the mutualism. Our findings therefore suggest a novel mechanism that allows for traits that facilitate a mutualism to evolve in response to selection and be maintained amidst a background of more common periods when one species is usually an antagonist.

One possibility is that masting may be an adaptive strategy of bird-dispersed pines to prevent local nutcracker populations from becoming too large (i.e. more birds per seed; Janzen 1976; Herrera *et al.* 1998, Kelly & Sork 2002), which in turn reduces the likelihood that nutcrackers persistently act as seed predators. Such interspecific population regulation has been argued as a mechanism to stabilize mutualisms in cases where one of the species acts as both an antagonist and mutualist (Holland *et al.* 2004). For example, when senita cactus (*Pachycereus schottii*) produces only a few flowers, its pollinator and seed parasite, the senita moth (*Upiga virescens*), consumes a high proportion of the seeds. This acts to destabilize the mutualism. When flower production is high, moth larvae consume a much lower proportion of the seeds, which benefits the plant and ultimately acts to

maintain the mutualism (Holland *et al.* 2004). In contrast, stable seed/fruit production is favoured in vertebrate seed dispersal systems where the dispersers, unlike nutcrackers, do not consume seeds (Herrera *et al.* 1998).

#### 4. CONCLUSIONS

Our findings have broad implications for understanding both evolution in response to temporal variation in the environment and the consequences of such variation to the ecological and evolutionary dynamics of species interactions. First, our results indicate that infrequent selection imposed by varying environmental conditions can be important for shaping the evolution of traits and species interactions. Since the seed pulse caused by masting is a prominent source of environmental variation for both seed dispersers and seed predators of many plants (Janzen 1976; Herrera *et al.* 1998; Ostfeld & Keesing 2000; Kelly & Sork 2002; Vander Wall 2002; Jansen *et al.* 2004), we suspect it may be a widespread factor underlying the tempo of adaptive evolution of plant reproductive traits via their interactions with seed consumers. Our results reveal a novel consequence of masting that should apply equally well to interactions with strict seed predators: that it mediates the intensity or opportunity for selection (figure 1c). Second, although temporal variation in the form of interspecific interactions may be common (Thompson & Cunningham 2002; Nuismer *et al.* 2003; Thompson & Fernandez 2006), our results indicate that this variation does not always correspondingly translate into microevolutionary processes (i.e. nutcrackers may be antagonists, but during such times they exert weak or no selection) capable of driving trait evolution. Infrequent events can thus be more important than common events in shaping the long-term evolutionary trajectories of some species and their interactions with other species.

All research conformed to the guidelines set forth by the University of Wyoming Animal Care and use committee.

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