

Exploration and exploitation of foraging patches by desert sparrows: environmental indicators and local evaluation of spatially correlated costs and benefits

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Conventional evolutionary and behavioral reasoning expects foragers to show strong spatial preferences in environments with heterogeneous resource distribution. Moreover, consumers should benefit from exploiting the information embedded in environmental features that indicate resource abundance. In desert soils seed abundance associates strong and reliably with vegetation and litter cover at small spatial scales. However, other spatially correlated factors (substrate complexity, temperature, predation risk) may affect foraging costs, benefits and decisions by ground-feeding granivores. We used a sequence of three semi-controlled field experiments of binary spatial choice within a portable aviary to identify the main cause of foraging microhabitat selection by the most abundant postdispersal granivorous bird in the central Monte desert (Argentina). In the first experiment we placed the aviary at field to offer pairs of adjacent microhabitats of unmodified, naturally-contrasting substrates and environmental conditions to single, untrained rufous-collared sparrows *Zonotrichia capensis*. Birds selected covered microhabitats in winter and summer, ruling out substrate complexity or thermoregulation as main single causes of patch selection. The other two experiments dissociated seed abundance, tree cover and litter to reveal their effects on patch selection. The results indicate that 1) sparrows do not restrict microhabitat exploration relying on environmental indicators, 2) distance to tree cover influences the order of patch exploration, probably in association with apprehension or risk-assessment behavior, and 3) patch exploitation is determined by short-term local estimation of seed abundance. The integration of these with previous results obtained under variable degrees of realism and experimental control allows for a better explanation of the spatial component of postdispersal granivory and its consequences on plants. The unconstrained selective foraging strategy of these sparrows would allow them to detect sporadic or ephemeral rich patches with structural characteristics indicating 'low-quality', should promote the spatial homogenization of the palatable seed bank, and would favor indirect interactions between plants.

A number of factors can affect the selection of foraging places by small animals. At microhabitat or patch scale, the main costs and benefits should be determined by food availability, foraging efficiency, vulnerability to predators, and microclimate (Wiens 1985, Repasky and Schluter 1996, Meyer and Valone 1999). The decision-making process of the foraging animals involves gathering information on those factors, either by inference from reliable environmental indicators or by local assessment after the site has been explored (Mitchell 1989, Stephens 2007). Most modelling and empirical efforts have been devoted to unveil the processes by which foragers decide how much a random-accessed patch should be (optimally) exploited, for example combining previous expectations with local while-foraging assessments (e.g. Bayesian foragers: Valone 2006, Olsson and Brown 2010). However, behavioral responses of individual foragers have proved context dependent (Gordon 2011): state-dependent, time-dependent and

variance-sensitive, varying with contingencies such as physiological state, environmental conditions and population and community properties (e.g. abundance, predators, competitors; Ydenberg et al. 2007). As a consequence, the actual importance of each of the potential causal factors is not obvious under complex, natural field variability in both environmental and individual conditions. The expected global foraging patterns, i.e. those that have consequences on resources, remain elusive or ambiguous, hindering our ability to understand resource–consumer reciprocal effects and to predict their responses to changing conditions.

Though many external and internal factors may eventually have an influence on individual foraging decisions, consumers are expected to show strong spatial preferences when foraging in environments where food availability is highly heterogeneous and correlated with informative environmental features. This is the usual scenario with seeds, litter and woody vegetation in desert soils. In deserts, seed

availability is highly heterogeneous in the soil and associates persistently with vegetation structure at small spatial scales (Price and Reichman 1987, Guo et al. 1998). For example, in the algarrobal of the Biosphere Reserve of Ñacuñán (central Monte Desert, Argentina), an open woodland of algarrobo *Prosopis flexuosa* trees, most of the floristic and structural heterogeneity at microhabitat scale relates to shrub and tree cover (Milesi 2006), and seed abundance and litter accumulation are consistently higher in the soil under them (Marone and Horno 1997, Marone et al. 2004). This association turns woody cover into putative conspicuous visual cues of resource abundance which, according to conventional evolutionary and behavioral reasoning, should be used by granivores as proximate factors for enhanced foraging efficiency and allocation of energy. In more general terms, consumers should benefit from information available or gathered at low-cost (Olsson and Brown 2010) enabling them to follow a strategy of guided patch selection on simple rules (e.g. 'only explore patches under woody cover') instead of the less-informed procedure of random patch search followed by patch departure decisions conditional on local estimations of quality. This should free birds of the costs associated with indiscriminate exploration, involving both the costs of traveling among patches and the opportunity cost of not exploiting better patches while busy estimating the suitability of each poor patch (Kohlmann and Risenhoover 1998, Olsson and Molokwu 2007, Sih 2011). However, the predicted spatial association between vegetation cover and postdispersal seed consumption was not as evident as presumed when tested at field in our study site: no differences in vegetation characteristics were found between foraging microsites of granivorous birds and randomly chosen microsites (Milesi et al. 2008). In fact, birds removed single experimental seeds more frequently in open microhabitats which associate with low-quality patch characteristics (Milesi 2006).

Several non-exclusive explanations can account for these unexpected patterns. One of them is that other factors, also strongly correlated with woody vegetation cover, involve foraging costs that reduce the net benefit of foraging in rich patches. Litter accumulated under woody plants is a reliable indicator of higher seed abundance (litter traps most seeds during secondary dispersal) but could also be a poor foraging substrate to detect and capture seeds (Whalen and Watts 2000, Whittingham and Markland 2002, Cueto et al. 2013). There are also large temperature differences between exposed and shadowed sites, and small birds should avoid the highest temperatures under direct solar radiation of exposed microhabitats in summer ($> 35\text{--}40^\circ\text{C}$) to reduce their metabolic rate and, particularly, to diminish evaporative water loss (Wolf and Walsberg 1996, Wolf 2000, Williams and Tieleman 2001). Previous results in this same area showed higher diurnal seed removal in covered microhabitats in summer but not in winter (Lopez de Casenave et al. 1998), which may result from birds extending their summer foraging activity towards hot middays (when they usually rest perched under cover) to exploit the exceptionally profitable offer of artificial ad libitum trays in shaded patches. Finally, perception of predation risk in association with vegetation cover is usually invoked to explain the selective use of space by small birds (Schneider 1984,

Watts 1991, Repasky and Schluter 1994, Carrascal and Alonso 2006, Molokwu et al. 2010), even though a particular selective pattern based on actual risk of predation cannot be easily predicted (Lazarus and Symonds 1992, Lank and Ydenberg 2003) and its relative importance can differ according to species-specific characteristics of both predators and prey (Pulliam and Mills 1977, Lima 1990, Carrascal and Alonso 2006).

Experimental tests of foraging theory have revealed the subtlest details in the decision-making mechanisms of some model animals (Stephens et al. 2007), though usually sacrificing realism (e.g. standardized settings to match model assumptions, reduced variability of resources and conditions, loss of field context, training or baiting of experimental subjects to force their patch-choice) to reveal behavioral or cognitive capabilities rather than eliciting usual field behaviors. Conversely, observational field studies provide good descriptions and retain context but are ill-suited to distinguish among spatially correlated factors or mechanisms that may produce similar spatial patterns. Controlled field experiments with realistic values of significant variables (Petraitis 1998) and embracing natural variability (Polis et al. 1998) are called for, not only to enhance extrapolative power and comparability to natural conditions (see, e.g. the series by Repasky and Schluter 1994, 1996 and Repasky 1996) but also because embracing variation proves essential for the development of ecological theory (Scheiner and Willig 2011).

In this work our objective was to detect the most relevant single or interacting factors that associate with foraging microsite preferences by the rufous-collared sparrow *Zonotrichia capensis*. This is the most abundant seed-eating bird in the central Monte desert, feeding mostly on grass and forb seeds from the seed bank after their dispersal by wind and rain at the end of summer (i.e. a postdispersal granivore; Lopez de Casenave 2001, Milesi 2006, Milesi et al. 2008). We used a behavioral tool (recording behavioral states and events of focal individuals in experiments of spatial choice) for an ecological question within a series of field studies of foraging site selection by granivorous birds and its consequences in the Monte desert (Milesi 2006). As many factors of both environment and consumers are expected to have some influence on patch selection, inter-individual and environmental 'noises' were deliberately included in the experimental design to test if expected selective patterns are still evident at the habitat level in spite of natural sources of variability. We did three sequential semi-controlled experiments of binary spatial choice in a portable field aviary. In experiment 1 we placed the aviary in the field in such a way to offer pairs of adjacent microsites of naturally-contrasting characteristics to single, untrained *Z. capensis* individuals, to test if there is a general pattern of foraging site selection at this scale and evaluate its association with both foraging benefits (food abundance) and costs (thermoregulation, substrate complexity, predation risk). In the other two experiments we further explored the selective pattern by breaking the spatial association of some of those conditions within the aviaries to evaluate if birds rely on different environmental cues of patch quality or assess patch profitability during patch exploitation.

Methods

Study area

The study was done in the Biosphere Reserve of Ñacuñán (34°03'S, 67°54.5'W), in the central Monte desert (Mendoza, Argentina). The main habitat of the Reserve is the 'algarrobal', an open woodland of algarrobo *Prosopis flexuosa* trees, usually 3–6 m high, scattered over a matrix with high cover of perennial tall shrubs (>35% cover, 1–3 m high, mostly *Larrea divaricata*) and of perennial grasses (>25%). About a third of the surface of the algarrobal are open patches of different size (decimeters to few meters). Seed abundance in the soil is very heterogeneous at small scales, with patches of extreme abundances close in space. Seeds are consistently and permanently more abundant under trees and shrubs and in depressions of the soil, where litter accumulates (Marone et al. 1998, 2004). Maximum availability of seeds occurs in autumn–winter, with a minimum when summer starts. For an extended description of the study area, and seed and vegetation heterogeneity see Lopez de Casenave (2001) and Milesi (2006).

General experimental design

Selection of foraging microsites by single *Z. capensis* birds was studied under a semi-controlled protocol along three sequential experiments of binary choice in portable field aviaries. The open bottom of the aviary (2 × 1 × 1 m) was considered divided in two halves, with a transversal horizontal perch at 25 cm height in between. This 'patch size' broadly agrees with the spatial scale used in associated local field studies of the seed bank and bird foraging (Marone et al. 2004, 2008, Milesi et al. 2008, Cueto et al. 2013).

In total, 55 birds were captured with mist-nets and kept in individual cages under natural photoperiod, with ad libitum *Setaria italica* seeds and water. A brief fasting period (2–2.5 h) was forced before trials (after early morning feeding). Individuals were not selected or trained before experiments, and time between capture, test and release was minimized (usually 1–2 d, maximum = 7 d) to prevent birds from changing their food preferences, physiological condition or getting habituated to captivity (Butler et al. 2006). We assume that inter-individual variation in previous field experience, physiological conditions and behavioral responses at the field population were represented in the experimental population. Each bird was trialed only once and released immediately afterwards.

Each individual was released in the center of the aviary from a remotely-opened small box. Trials were videotaped from behind one of two blinds (vertical green cloths) at 2–4 m from each long-side of the aviary. Tapes were digitized and analyzed at ×0.5 speed, recording foraging events (pecks and scratches) and behavioral states (the horizontal and vertical position of the bird). In the vertical axis, two exclusive states were defined: 'on the ground' and 'lying/perched'. In the horizontal axis, two sectors of the aviary were defined: 'covered' (CO, under an algarrobo tree) and 'exposed' (EX). Moving to the central perch was not considered a change of sector. Foraging events recorded were: 'peck', when the bird pecked the ground (independently of the inferred goal or the result), and 'scratch', when the bird removed soil or litter

with a sudden simultaneous movement of both legs ('bilateral scratching' or 'double-scratching'; Greenlaw 1977). We defined foraging bouts as periods in which the bird was actively searching and consuming food, according to the combination of states and events recorded. We operationally established a foraging bout (similarly to Whittingham et al. 2004) as the continuous time interval with ≥ 5 foraging events during ≥ 5 s without leaving the ground or > 10 s between successive events. Intervals of 5–10 s between successive events were only considered the end of a foraging bout when bird activity was not related to foraging (e.g. running along an aviary border, pecking the wire, preening). Following these criteria, foraging bouts included 92.4% of the pecks and 97.2% of the scratches recorded in all the experiments. Foraging bouts and events were assumed as proxies for intensity of seed predation. Though natural substrate and field set-up hindered more precise measurements (e.g. successful ingestion of every food item), we confirmed through video records that most pecks within foraging bouts corresponded to active seed consumption as expected. Trials were finished 720 s (= 12 min) after the first foraging bout started (in a few cases where the film record lasted 10–12 min the values were extrapolated multiplicatively to 720 s for easier comparisons). Trials in which birds did not start foraging in the first 30 min since leaving the releasing cage (latency) or in which total foraging time was less than 90 s (12.5% of the trial) were discarded as not providing enough evidence of foraging site selection.

Experiment 1: spatial preference of selected natural conditions

Foraging microsite selection was evaluated in summer and winter under semi-controlled natural conditions. Trials were done in windless sunny mornings (between 10:45 and 13:00, local solar midday ≈ 13:30), during both winter (July–August 2000) and summer (December 2000 and February 2001), each in a different aviary location at field. Aviary locations were selected to include two adjacent naturally-contrasting microsites that co-occur in the general habitat: one half was under algarrobo canopy, with naturally accumulated litter and tree shade at the beginning of each trial (CO), and the other exposed, with bare ground and direct sunlight (EX). No modifications were made except for removing occasional herbaceous plants. Temperature of soil surface was measured in the center of each sector with a digital thermometer 1) to confirm its strong association with degree of insolation depending on season and 2) to be used as a surrogate of thermoregulatory stress for the animals (which also depends on other factors: Wolf et al. 2000, Williams and Tieleman 2001) among markedly different conditions. Four soil samples (3 cm diameter and 1 cm depth) were taken before every trial in the corners of a 50 cm-square centred in each sector (i.e. eight samples per aviary location). Samples were processed and examined for presumed viable seeds following protocols and criteria in Marone and Horno (1997) and Marone et al. (2004). Consumable seeds for *Zonotrichia capensis* were defined according to a local, long-term diet study: all grass species plus forbs in the genera *Chenopodium*, *Sphaeralcea*, *Parthenium* and *Heliotropium* (Lopez de Casenave 2001). Available seed biomass (g m⁻²) was

calculated using mean seed weights per genus taken from Peralta and Rossi (1997), Marone et al. (1998) and Lopez de Casenave (2001).

If there is a general selective pattern prevailing over individual particularities of both birds and locations and the main mechanism of foraging patch selection does not change between seasons, three exclusive patterns are expected, depending on the single most important factor at this scale: 1) if selection of foraging sites depends mainly on seed abundance (either directly measured or inferred through environmental cues), birds should prefer the higher seed abundance and biomass in sector CO in both seasons; 2) if seed detectability or accessibility, and consequently searching or handling efficiency, are crucial factors (Getty and Pulliam 1993) birds should prefer the bare ground in EX in both seasons since foraging success is negatively affected by litter accumulation (Cueto et al. 2013); and 3) if selection is constrained by thermoregulation costs or body water loss, birds should avoid direct sunlight in EX in summer (when exposed ground is $> 35^{\circ}\text{C}$) but show no sector preference in winter (when temperature is similarly low in both sectors) or a slight preference for EX to reduce their metabolic rate.

Fifteen *Z. capensis* individuals in winter and 16 in summer were captured and tried; two birds per season failed to feed in the first 30 min in the aviary, while one trial in winter and two in summer were discarded a posteriori due to short foraging time (< 90 s). Consequently, 12 trials per season were considered valid for analysis.

Experiments 2 and 3: dissociation of correlated environmental cues and actual seed offer

In these experiments the aviary was also placed in the field but the conditions were modified to disentangle various correlated environmental cues and dissociate them from actual seed availability to unveil the main mechanism of patch selection previously observed (experiment 1). In experiment 2 natural seed abundance was swapped between sectors. If birds rely on environmental cues (tree cover, litter accumulation) as indicators of patch quality they should keep the spatial preference shown in experiment 1, whereas if micro-site preference is based on the local evaluation of seed offer during exploration, then birds should prefer the more profitable sector (now EX). In experiment 3, those two correlated environmental cues that may be guiding the initial choice of a foraging microsite to explore were dissociated by moving the litter to EX while seed offer was equalized. If birds use tree cover as a guide they should prefer CO but if the key cue is litter they should prefer EX, while if foraging patch selection only depends on seed offer birds should show no sector preference.

Before each trial of experiment 2 the natural substrate on sector CO was replaced with the 'seed-impovertished' bigger litter fraction that remained on a sieve (~ 5 mm mesh) coming from 1 m² surface soil under an algarrobo tree. The smaller (seed-rich) fraction, plus a few seeds of *Setaria italica* (200 seeds m⁻² = 0.52 g m⁻²; 2.3% of the average winter abundance of consumable seeds in litter under algarrobos, see Results for experiment 1), was placed on the bare ground of EX and covered with a shallow layer of fine ground for natural bare-ground appearance. Two samples of seed abundance per sector (25 cm to each side of their centres)

were taken before each trial and processed as explained for experiment 1 to confirm the required conditions. Eleven individual birds were tested between 10:30 and 13:45 h in winter (July 2001) to keep similar insolation in both sectors and avoid stressful temperatures. Briefly, contrasting conditions in aviary sectors were: CO (covered/litter/less seeds) vs EX (exposed/bare ground/more seeds), with similar temperature and insolation. One bird failed to forage in the first 30 min and another foraged for < 90 s, with nine trials remaining valid for analysis.

Experimental design and protocol were similar in experiment 3, except that the sieved bigger portion of litter from 1 m² under an algarrobo tree was more intensively sieved before locating it in EX, farthest from the tree (the smaller fraction of litter containing most seeds was discarded). Soil from a near area of bare ground, sieved through a 0.3 mm mesh to remove all seeds, was placed in CO. Two hundred *Setaria italica* seeds were scattered in each sector (0.52 g m⁻²), and covered with a thin layer of seedless soil in CO mimicking bare-ground appearance. Binary choice in this experiment was reduced to CO (covered/bare ground) vs EX (exposed/litter), with similar temperature and seed abundance in both sectors. Thirteen trials were done in July and August 2001, though 10 were analyzed after discarding two birds that foraged < 90 s and one trial with film record damaged.

Statistical analyses

We estimated foraging intensity as the foraging time and the number of pecks (within every foraging bout) per aviary sector in each trial with a different individual bird. Selection of a foraging sector between the two available options was evaluated as the proportion of total foraging time and of the number of pecks in the covered sector of the aviary (e.g. $P_{\text{CO}} = 1$ if the bird only foraged in CO, $P_{\text{CO}} = 0.5$ if there was no preference). We estimated sector preference during latency time as the proportion of time spent in each sector since the bird left the cage until the first foraging bout.

Tests based on one data value per aviary sector (seed abundance and biomass, temperature, foraging time, number of pecks) were analyzed with random-intercepts linear mixed models to account for the hierarchical structure (i.e. a split-plot design of sectors within aviaries) while allowing for different levels of mean aviary conditions and individual responses (e.g. individual bird foraging activity). Some measured variables were square-root- (foraging time) or log- (number of pecks and number and biomass of seeds, after adding the minimum possible measured value to avoid zeroes) transformed in order to assume normality of residuals and random factors, which was graphically checked (using qqplots, scatterplots and boxplots of residuals). Residual variances were checked for homogeneity and modeled as heterogeneous when adequate. The small datasets prevented fitting more theoretically appropriate but data-demanding models (e.g. finite mixture models or compound distributions).

Analyses from single integrative values at the aviary level (proportions of time, events and seeds) were also modeled with generalized least squares for methodological coherence with the analyses above and to allow for variance heterogeneity if relevant. Proportions were analyzed in the logit scale

after minimum rescaling to avoid observed zeros and ones (smallest measurable value added or subtracted, respectively; Warton and Hui 2011). In the simplest case of analyses of proportions with no predictive factors (experiments 2 and 3 and reduced models in experiment 1) this reduces to test the null hypothesis that $P_{CO} = 0.5$ or $\text{logit}(P_{CO}) = 0$. All results are presented after back-transformation to proportions.

Statistical analyses were done within R (R Core Team) running on RStudio Desktop for Linux (RStudio Team 2012), using the `lme` and `gls` functions in the `nlme` package (Pinheiro and Bates 2000, Pinheiro et al. 2013). We followed the general top-down modeling approach suggested by Zuur et al. (2009), selecting the random structure for saturated fixed models and then comparing nested models which simplify the fixed structure for unsupported parameters by deleting explanatory variables. The depleted (simpler) model was compared with the full (reference) model estimated by restricted maximum likelihood (REML, for tests of heterogeneous variabilities between models with the same fixed structure) or by maximum likelihood (ML, for tests of fixed factors between models with the same random structure). Deletion tests are reported as ‘Variables’ where Variables declare those parameters that differed between reduced and reference models, followed by the difference of Akaike’s information criterion (ΔAIC) and the likelihood ratio test (L) with its associated degrees of freedom and corresponding p -value. Small ΔAIC , low L and high p -value suggest model simplification (i.e. not enough empirical support to sustain the more complex model). Parameters of final models reported were estimated by REML. For Wald-tests, t statistics associated with null hypotheses of $\text{logit}(P_{CO}) = 0$ are reported with their degrees of freedom and p -values. Measured ranges are reported between brackets after mean values, while 95% confidence intervals on estimated values (conditional on random factor where appropriate) are abbreviated as CI.

Results

Experiment 1

Conditions of ground temperature and seed availability in adjacent natural microhabitats, selected by locating the experimental aviaries at field, confirmed presumed contrasts. Differences in ground temperature between aviary sectors, associated with insolation, differed between seasons (Season \times Sector: $\Delta AIC = 28.29$, $L_1 = 30.287$, $p < 0.001$). In summer, when differences were big ($\Delta = 13.9$ [9.7–18.8] $^{\circ}\text{C}$), EX temperature (42.5 [35.8–52.5] $^{\circ}\text{C}$) was always above the critical threshold of water loss by evaporation for small birds (Wolf and Walsberg 1996, Wolf 2000). In winter, aviary sectors were more similar ($\Delta = 5.9$ [1.6–9.9] $^{\circ}\text{C}$) and both within the tolerable range for the birds (11.9 [6.3–19.7] $^{\circ}\text{C}$). The estimated abundance (and biomass) of consumable seeds was higher in the litter of CO sector than in the bare ground of EX in every single position of the aviary in the field, in both seasons. That difference did not depend significantly on Season (Season \times Sector and Season: $\Delta AIC = -2.03$, $L_2 = 1.970$, $p = 0.373$). The estimated mean abundance (i.e. a geometric mean or log-average) was > 20 times higher in

CO (5467.7 seeds m^{-2}) than in EX (254.3 seeds m^{-2}). An even bigger difference (> 40 times higher) was evident by estimating seed biomass (1.537 vs 0.037 g m^{-2} , respectively).

Even when not selected or trained, birds responded promptly to the experimental setup. They remained on the ground most of the time after starting to forage (631 [160–720] s), foraging for, on average, over half of the length of the experimental sessions (413 [103–720] s). Latency time was higher during summer (Season: $\Delta AIC = 3.53$, $L_1 = 5.534$, $p = 0.019$; summer = 105.9 s, winter = 28.7 s), with sector preference (proportion of latency time) very variable among individuals but with a general tendency towards preferring CO sector in both seasons (Season: $\Delta AIC = -1.41$, $L_1 = 0.588$, $p = 0.443$; $P_{CO} = 0.848$, CI = 0.477–0.972).

Foraging in the aviaries was positively associated with seed availability in each aviary sector, independently of Season (Season \times Seeds and Season: $\Delta AIC = -3.62$, $L_2 = 0.382$, $p = 0.826$) when estimated as the relation between number of pecks and seed number (Seeds: $\Delta AIC = 29.69$, $L_1 = 31.690$, $p < 0.001$). The result is very similar, and also independent of Season (Season \times Seeds and Season: $\Delta AIC = -3.48$, $L_2 = 0.522$, $p = 0.770$) between foraging time and seed biomass (Seeds: $\Delta AIC = 33.54$, $L_1 = 35.539$, $p < 0.001$; Fig. 1). However, those strong relationships became non-significant when Sector was included as a main explanatory factor, i.e. there was no further association between foraging intensity and the availability of seeds over and above their mean values for each microhabitat type (Seeds [with Sector in the model]: for number of pecks: $\Delta AIC = -1.99$, $L_1 = 0.011$, $p = 0.917$; for foraging time: $\Delta AIC = -1.99$, $L_1 = 0.014$, $p = 0.905$).

Every individual bird explored the ground of sector CO and most (16/24) explored the ground of EX; in approximately half of the aviaries (13/24) they actually foraged in both sectors. However, bird foraging in sector EX was

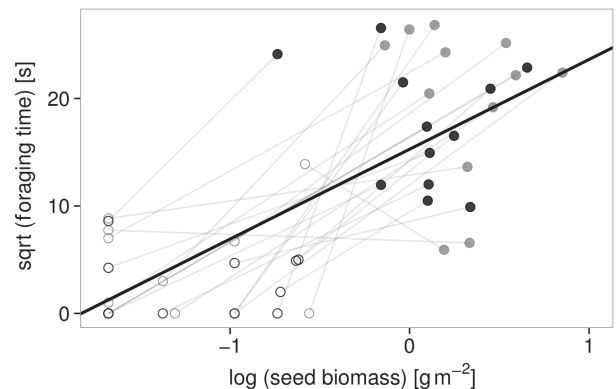


Figure 1. Foraging intensity by *Z. capensis* individuals (foraging time) against natural seed availability (estimated seed biomass) in the substrate of the covered (full circle) and uncovered (empty circle) sectors of the field aviaries during summer (black) and winter (grey) trials of experiment 1. Black line shows the overall regression, and grey lines connect the values of the two aviary sectors in each trial (with a different bird in a different position at field). Note that seed availability in CO sector was always higher than in EX sector at every aviary position. A very similar figure results from estimating foraging intensity as number of pecks and natural seed availability as seed density (not shown).

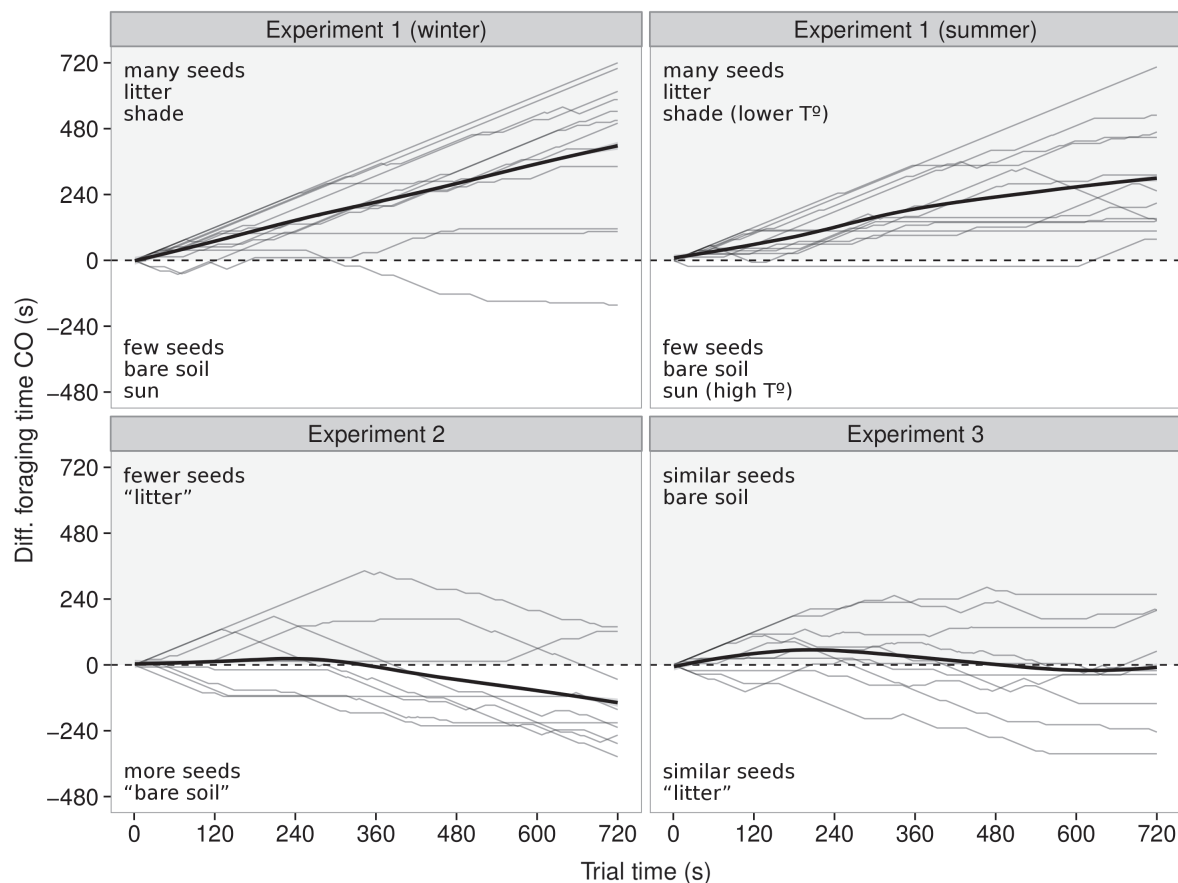


Figure 2. Cumulative difference in foraging time between the two aviary sectors along the duration of each trial (720 s from the beginning of the first foraging bout), with positive values indicating a difference in favor of sector CO (i.e. the sector closer to the tree, in light grey). Other contrasting conditions between sectors are indicated for each experiment see text for details. Each grey line shows the foraging progression of an individual bird; lines go up during a foraging bout in sector CO, go down when foraging in EX, and stay horizontal when the bird is not foraging. The thick black line is a smoother on the mean value for the individual trials in each experiment.

usually brief, returning to CO for longer bouts (Fig. 2; detailed ethograms in Milesi 2006 or available from the corresponding author). Foraging time within the aviaries did not differ significantly among seasons (Season \times Sector and Season: $\Delta AIC = -2.11$, $L_2 = 1.887$, $p = 0.389$). Irrespective of season (Season: $\Delta AIC = -1.69$, $L_1 = 0.314$, $p = 0.575$), birds spent most of their foraging time in sector CO (estimated $P_{CO} = 0.986$, $CI = 0.957-0.995$, $t_{23} = 7.889$, $p < 0.001$; Fig. 2). Almost identical conclusions result when inferring foraging success from the number of pecks (Season \times Sector and Season: $\Delta AIC = -1.87$, $L_2 = 2.131$, $p = 0.345$; CO = 220.28 pecks, EX = 4.38 pecks) and when analyzing their proportion within each aviary (Season: $\Delta AIC = -1.32$, $L_1 = 0.128$, $p = 0.720$; estimated $P_{CO} = 0.985$, $CI = 0.954-0.995$, $t_{23} = 7.573$, $p < 0.001$).

Birds 'double scratched' to search for seeds almost exclusively in CO where litter was present, and 5.5 times more frequently in winter. In fact, foraging activity as a whole was more intense in winter trials (Fig. 3). Mean peck rate during foraging bouts in each sector did change between seasons (Season \times Sector: $\Delta AIC = 2.48$, $L_1 = 4.484$, $p = 0.034$): foraging in the CO sectors was $\sim 30\%$ slower in summer trials (winter: 0.92 pecks s^{-1} ; summer: 0.63 pecks s^{-1}), while it remained intermediate and similar in the few measured bouts in the EX sector (~ 0.8 pecks s^{-1}).

Experiments 2 and 3

Experimental dissociation of substrate and seed abundance was effective and inverted seed abundance and biomass between sectors for experiment 2 (Sector: seed

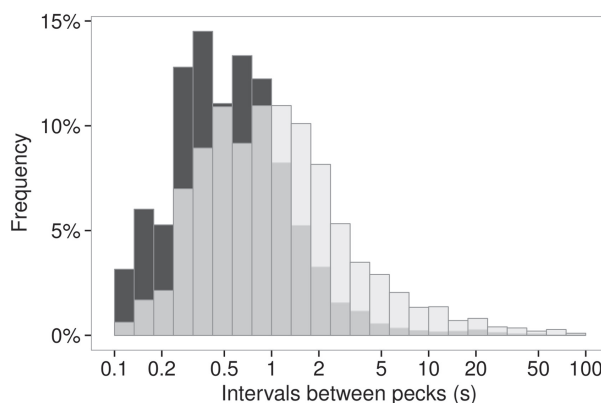


Figure 3. Frequency distribution of time intervals (in log-scale) between successive pecks for all the winter (dark grey) and summer (light grey) trials of experiment 1. Intervals < 5 s were interpreted as within the same foraging bout (see text).

abundance: $\Delta AIC = 3.38$, $L_1 = 5.380$, $p = 0.020$; seed biomass: $\Delta AIC = 10.64$, $L_1 = 12.64$, $p < 0.001$). Mean values resulted within the natural range, but now 3–8 times higher in the simulated ‘bare-ground’ of EX sector (EX: 2179 seeds m^{-2} , 1.151 g m^{-2} ; CO: 745 seeds m^{-2} , 0.144 g m^{-2}).

General parameters of foraging activity (time on the ground, foraging time, number of foraging bouts, peckrate) were similar to those in winter trials on the natural substrates of Experiment 1, but foraging preferences were radically different. Even when birds still preferred the CO sector before starting to forage ($P_{CO} = 0.892$, $t_8 = 2.477$, $p = 0.038$), and most (7 out of 9) did start foraging in the littered sector closer to the tree, almost all of them moved eventually (15–485 s later) to forage preferentially in EX without returning to forage in CO for substantial periods (Fig. 2). As a consequence, detected preferences for EX sector increase with the (arbitrary) length of the trials. Results for the total experimental time revealed no global Sector preference ($P_{CO} = 0.357$, $t_8 = 0.703$, $p = 0.502$) unless an outlier corresponding to the only individual that did not try the modified substrate in EX is removed (without #7: $P_{CO} = 0.207$, $t_7 = 3.347$, $p = 0.012$). The preference for EX was much stronger when evaluated for the second half of the experiments (Fig. 2), when most individuals had tested both foraging patches (again, removing the outlier #7: $P_{CO} = 0.08$, $t_7 = 8.873$, $p < 0.001$). As in the previous experiment, the same conclusion results from analyzing foraging effort per Sector as the amount of foraging time or as the number of pecks (not shown).

During trials of experiment 3, most birds (7/10) started foraging in sector CO (closer to the tree but now with no litter) following a similarly variable trend to occupy that same sector during latency ($P_{CO} = 0.858$, $t_9 = 1.502$, $p = 0.167$). In spite of that, birds did forage in both sectors, with no sector preference detected for the total length of the trials ($P_{CO} = 0.389$, $t_9 = 0.615$, $p = 0.554$; Fig. 2) nor for the second half of the experiment ($P_{CO} = 0.260$, $t_9 = 1.241$, $p = 0.246$), even when removing the single bird that foraged in just one sector ($P_{CO} = 0.365$, $t_8 = 0.724$, $p = 0.490$).

Discussion

The correlation between resource abundance and use is a default assumption or prediction of classic foraging models focused on bottom-up effects (Pyke 1984, Stephens and Krebs 1986, Sih 2011) since it agrees with the simplest expectations on behavioral or evolutionary grounds (i.e. animals learn or are selected to forage where profitability is higher). But even if this simple selective pattern is verified, mechanisms affecting the decision-making process of the animals may still remain elusive because: 1) food abundance and its reliable indicators covary, and they may be spatially associated with factors that also influence patch quality (i.e. adding costs or benefits), and 2) the stage at which a selective decision is taken may not be evident (e.g. as guided patch exploration or as random exploration with local instantaneous assessment and giving-up rules). We used a sequence of experiments in a semi-controlled, realistic setup, starting from unmodified, naturally-contrasting field conditions, to isolate the main factor and mechanism

involved in foraging microhabitat selection by the rufous-collared sparrow *Zonotrichia capensis*, the most abundant seed-eating bird in the central Monte desert.

Most of the recently-captured, untrained individuals of *Z. capensis* did show a strong general selective pattern over and above individual, spatial, and seasonal variations. Birds selected covered aviary sectors as expected by the simplest hypothesis that seed offer determines directly or indirectly the selection of a foraging patch. Without further experimental manipulations this preference may be also interpreted as caused by tree cover (or closeness) or accumulated litter by themselves or as surrogates of other correlated factor that modify foraging costs or benefits at the microhabitat scale (e.g. a lower perceived risk of predation). However, other potentially relevant simple factors proved not as important. Birds did not avoid complex substrates in spite of their lower foraging efficiency on litter (Cueto et al. 2013), mitigated by the ability of this species (and other sparrows: Greenlaw 1977, Whalen and Watts 2000) to reach buried seeds by ‘scratching’ the superficial substrate with their legs. Although high summer temperature diminished general foraging activity (e.g. birds failed to forage or forage for the shortest time when temperature in the shade was $> 37^\circ C$, a consistent result with those of field seed removal experiments, Milesi 2006), microhabitat preference by *Z. capensis* was still strong in experiments carried out in winter, when direct insolation should not entail negative consequences. Thus, ground temperature or direct insolation and their effect on thermoregulation do not seem necessary or sufficient to explain the selective spatial pattern found.

Postdispersal seed predation, as other foraging situations, can be split in two components: 1) patch exploration, the probability of at least one seed being removed from a patch, and 2) patch exploitation, the amount or proportion of seeds removed once the patch was explored (‘seed encounter’ and ‘seed exploitation’ sensu Hulme 1994). In the algarrobal of Nacuñán, where the spatial distribution of seed can be predicted all year round (Marone et al. 2004, this work), granivorous birds should increase their foraging success by using visual, remotely-perceivable environmental surrogates that provide reliable information on patch profitability. This would allow them to neglect poor patches before going through the information cost of their exploration, as predicted by ‘attack’ foraging models like the classic ‘optimal patch choice’ and ‘diet’ models (Pyke 1984, Stephens and Krebs 1986, Ydenberg et al. 2007). However, when the abundance of seeds was swapped between sectors for the trials of experiment 2, the strong preference for sector CO observed under natural conditions (experiment 1) reverted: birds foraged preferentially where they (quickly) detected that seed abundance was higher (i.e. sector EX with ‘bad’ values of natural indicators). This is to be expected if *Z. capensis* individuals are deciding on where to forage by the local evaluation of patch quality during patch exploitation. Results from experiment 3 strengthened the hypothesis that seed abundance is the main factor being evaluated: with similar seed abundances in both aviary sectors, birds did not repeat the previous patch preference, even when the other potentially relevant factors in this experimental setup (litter, tree cover) were still present. In fact, most birds in the three experiments frequently explored the alternative sector of the aviary even

when seed abundance in the initially exploited sector was high, and any explored sector was quickly abandoned when it had few seeds. So, despite the strong correlation between seed abundance and several environmental factors in this habitat, individual birds did not restrict their exploration of microhabitat and, instead, used a persistence–departure rule based on short-term local estimations of foraging success during seed search and consumption (i.e. the realm of ‘exploitation’ or classic ‘patch’ foraging models: Stephens and Krebs 1986, Ydenberg et al. 2007).

Tree cover or a shorter distance to a tree showed some non-restrictive influence on the initial exploration patterns of *Z. capensis* individuals in the aviaries. One interpretation from the results of experiment 2 is that foraging birds approach tree cover following a prior expectation of (high) seed abundance and then update the estimation while exploiting the patch to decide when to leave the patch (‘Bayesian foragers’; see McNamara et al. 2006 and other papers in that issue). However, litter is a better spatial predictor of seed bank abundance and composition than tree cover (Marone and Horno 1997) and it was not the clue guiding the initial exploratory stage as shown in experiment 3 (though the low number of trials may have prevented the detection of weaker spatial preferences after this initial response). An alternative interpretation that we favor is that algarrobo canopies are informative cues of foraging costs related to the perception of lower predation risk. Trees are regularly described as refuges, sites of lower perceived risk and frequent destination of birds flushed at field for many passerines (Pulliam and Mills 1977, Schneider 1984). According to the predation risk allocation hypothesis (Lima and Bednekoff 1999), birds may have perceived the start of the trials as a high-risk situation, delaying foraging to move towards a refuge from where evaluate danger (Sih 1992, Bednekoff 2007). Such apprehension or avoidance behavior is consistent with the idea that ‘fear’ also affects the use of space to forage (Lima and Dill 1990, Lima 1998, Brown and Kotler 2004, Cresswell 2008), and probably reflected the natural response of birds to episodic, periodical perception of threat. Many other studies have reported the preference of small birds for foraging closer to, though not necessary under cover (e.g. sparrows: Schneider 1984, Watts 1991, Repasky and Schluter 1994).

In conclusion, even when some environmental factors may influence on the probability or order of microhabitat exploration, individual *Z. capensis* sparrows seem to forage according to their short-term evaluation of seed availability in the patch being exploited. Birds are behaving as myopic foragers (sensu Mitchell 1989), ignoring the information embedded in the vegetation structure and litter to avoid low-quality patches and delaying the leave-stay decision until profitability is locally estimated, so paying ‘the penalty of ignorance’ (Olsson and Brown 2006). This decision-making process does not seem the optimal strategy for efficient seed predation under the apparently predictable spatial seed dynamics in the algarrobal of Nacuñán, and it is not obvious that birds are unable to perceive bold characteristics of the vegetation or to develop a patch-searching rule based on them. Local evolutionary adjustment may not be feasible or convenient because *Z. capensis* occupies a wide spectrum of habitats across the Neotropics, from forests to semi-deserts

to suburban gardens and city parks (Bellocq et al. 2011), and a fixed behavioral rule that maximizes foraging efficiency in this habitat may not hold as a good-enough rule-of-thumb in other habitats. Similarly, a learned foraging rule may be unattainable because part of the local population of *Z. capensis* is nomadic or migratory. Also, such a rule may not be as convenient as expected for two reasons. First, even when the association between seed bank and vegetation is strong and persistent in the algarrobal (Marone et al. 2004, this work), individual patches at the relevant scale for the birds may be more variable than we acknowledge as a consequence of consumption and secondary dispersion (and then the information that they provide would be less valuable; see Stephens 2007 on the value of information and the need for sampling). The costs of failed exploration may be counterbalanced by the occasional detection of rich patches that have structural characteristics associated with low-quality areas like the scattered depressions accumulating seeds in exposed areas, an usual feature in Nacuñán and other deserts (Price and Reichman 1987, Marone et al. 2004), or ephemeral patches of recently-dispersed grass seeds. This agrees with the big winter decrease in seed abundance in small natural depressions that accumulate seeds within bare-soil patches (Marone et al. 2004, 2008). Although expected foraging yield should be lower in temporally variable patch-types increasing the chance that the forager neglects them in favor of the predictable ones (Holt and Kimbrell 2007), when changes are fairly periodical and travel costs are not high the optimal strategy for the birds may be to frequently monitor all types of microsites (Krebs and Inman 1992). Second, the implicit assumption that birds move between more or less discrete patches at the scale we recognize through vegetation may not hold. Models of simultaneous movement and foraging in which foragers change speed and turns according to food abundance (Pyke 1984, Arditi and Dacorogna 1988) may be more appropriate to describe the exploration of the ground by walking granivorous birds like that of other grazing herbivores (WallisDeVries et al. 1999). Although some granivores can detect limits of patches differing in seed aggregation or abundance (Schmidt and Brown 1996, Fierer and Kotler 2000, this work), the distribution of patch qualities may defy the cognitive abilities of birds (Kohlmann and Risenhoover 1998) or their foraging scale may be much smaller than that at which vegetation provides useful information (Klaassen et al. 2006). However, in this experimental setup, with varying conditions among aviary positions in the field (experiment 1), absolute seed abundance was not a good predictor of foraging intensity within each microhabitat type (Fig. 1).

Factors affecting both exploration and exploitation of foraging sites need to be considered, along with the assumptions and focal stage within each experimental design, if we are to integrate partial results for a better explanation of the spatial component of postdispersal granivory. If we extrapolate the conclusions of these experiments to field conditions in the central Monte desert we should observe 1) no microhabitat providing a secure refuge for seeds, at least if they are defined only according to plant structure, 2) patches closer to trees having a higher probability of exploration, and 3) seed exploitation positively correlated to seed abundance in explored microsites. Two previous local studies found

support for the first two expected patterns: a single-seed removal field experiment that estimated the patch exploration component by birds (Milesi 2006) and a bird-centered analysis based on field observations of foraging granivorous birds that estimated both components of patch use (Milesi et al. 2008). The third field pattern was not directly evaluated yet in this habitat, and field techniques that evaluate patch exploitation by modifying the natural patterns of exploration (e.g. the GUD technique that attracts birds to highly profitable seed-trays; Brown 1988) may prove useful. An indirect support for this pattern is provided by Milesi et al. (2008), whose bird-centered analysis found no significant differences in vegetation characteristics between randomly-chosen and foraging microhabitats of *Z. capensis*, an expected result if birds explore open microhabitats more frequently – as found by single seed-removal experiments in Nacuñán (Milesi 2006) and in the Chihuahuan Desert (Thompson et al. 1991) – but spend more time foraging in profitable covered microhabitats. If this description of the spatial component of postdispersal granivory is correct, bird foraging would tend to homogenize the seed bank of palatable seeds at the microhabitat scale. They would visit all possible patches but forage selectively in the more profitable ones, which will tend to be depleted to the mean patch profitability at the habitat level (with the relationship between profitability and seed density secondarily affected by foraging costs related to predation risk, substrate or thermal loads).

Since local granivorous birds do show consistent seed preferences (Cueto et al. 2006, Marone et al. 2008), this foraging behavior may also induce indirect interactions between seed species and favor the coexistence of seeds occupying different microhabitats (Holt and Kotler 1987, Chaneton and Bonsall 2000, Veech 2000, 2001). For instance, birds that keep foraging in patches with enough preferred seeds may in the meantime consume more suboptimal (or less-preferred) seeds than if the latter had occurred alone in a patch triggering a 'give up' response. This is known as short-term apparent competition: the density of one species affects negatively the density or survival of the other through the behavioral response of their mutual predator. The opposite is apparent mutualism, such as preferred seeds finding 'refuge' in patches with abundant unpalatable or suboptimal seeds that deter bird foraging. Both kinds of predator-mediated interactions may affect the abundance and spatial distribution of grass and forb species whose recruitment is seed-limited, particularly given the tendency of some species or group of species to co-occur in the seed bank of the central Monte desert at the microhabitat scale (Marone et al. 2004).

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References

- Arditi, R. and Dacorogna, B. 1988. Optimal foraging on arbitrary food distributions and the definition of habitat patches. – *Am. Nat.* 131: 837–846.
- Bednekoff, P. A. 2007. Foraging in the face of danger. – In: Stephens, D. W., Brown, J. S. and Ydenberg, R. C. (eds), *Foraging: behavior and ecology*. Univ. of Chicago Press, pp. 305–329.
- Belloq, M. I., Filloy, J., Zurita, G. A. and Apellaniz, M. F. 2011. Responses in the abundance of generalist birds to environmental gradients: the rufous-collared sparrow (*Zonotrichia capensis*) in the southern Neotropics. – *Ecoscience* 18: 354–362.
- Brown, J. S. 1988. Patch use as an indicator of habitat preference, predation risk, and competition. – *Behav. Ecol. Sociobiol.* 22: 37–47.
- Brown, J. S. and Kotler, B. P. 2004. Hazardous duty pay and the foraging cost of predation. – *Ecol. Lett.* 7: 999–1014.
- Butler, S. J., Whittingham, M. J., Quinn, J. L. and Cresswell, W. 2006. Time in captivity, individual differences and foraging behaviour in wild-caught chaffinches. – *Behaviour* 143: 535–548.
- Carrascal, L. M. and Alonso, C. L. 2006. Habitat use under latent predation risk. A case study with wintering forest birds. – *Oikos* 112: 51–62.
- Chaneton, E. J. and Bonsall, M. B. 2000. Enemy-mediated apparent competition: empirical patterns and the evidence. – *Oikos* 88: 380–394.
- Cresswell, W. 2008. Non-lethal effects of predation in birds. – *Ibis* 150: 3–17.
- Cueto, V. R., Marone, L. and Lopez de Casenave, J. 2006. Seed preferences in sparrows species of the Monte desert: implications for seed-granivore interactions. – *Auk* 123: 358–367.
- Cueto, V. R., Milesi, F. A. and Marone, L. 2013. Litter and seed burying alter food availability and foraging efficiency of sparrow species in the central Monte desert, Argentina. – *J. Avian Biol.* 44: 339–346.
- Fierer, N. and Kotler, B. P. 2000. Evidence for micropatch partitioning and effects of boundaries on patch use in two species of gerbils. – *Funct. Ecol.* 14: 176–182.
- Getty, T. and Pulliam, H. R. 1993. Search and prey detection by foraging sparrows. – *Ecology* 74: 734–742.
- Gordon, D. M. 2011. The fusion of behavioral ecology and ecology. – *Behav. Ecol.* 22: 225–230.
- Greenlaw, J. S. 1977. Taxonomic distribution, origin, and evolution of bilateral scratching in ground-feeding birds. – *Condor* 79: 426–439.
- Guo, Q., Rundel, P. W. and Goodall, D. W. 1998. Horizontal and vertical distribution of desert seed banks: patterns, causes, and implications. – *J. Arid Environ.* 38: 465–478.
- Holt, R. D. and Kotler, B. P. 1987. Short-term apparent competition. – *Am. Nat.* 130: 412–430.
- Holt, R. D. and Kimbrell, T. 2007. Foraging and population dynamics. – In: Stephens, D. W., Brown, J. S. and Ydenberg, R. C. (eds), *Foraging: behavior and ecology*. Univ. of Chicago Press, pp. 365–395.
- Hulme, P. E. 1994. Post-dispersal seed predation in grassland: its magnitude and sources of variation. – *J. Ecol.* 82: 645–652.
- Klaassen, R. H. G., Nolet, B. A. and De Fouw, J. 2006. Intake rate at differently scaled heterogeneous food distributions explained by the ability of tactile-foraging mallard to concentrate foraging effort within profitable areas. – *Oikos* 112: 322–331.
- Kohlmann, S. G. and Risenhoover, K. L. 1998. Effects of resource distribution, patch spacing, and preharvest information on foraging decisions of northern bobwhites. – *Behav. Ecol.* 9: 177–186.
- Krebs, J. R. and Inman, A. J. 1992. Learning and foraging: individuals, groups, and populations. – *Am. Nat.* 140 (Suppl.): S63–S84.

- Lank, D. B. and Ydenberg, R. C. 2003. Death and danger at migratory stopovers: problems with 'predation risk'. – *J. Avian Biol.* 34: 225–228.
- Lazarus, J. and Symonds, M. 1992. Contrasting effects of protective and obstructive cover on avian vigilance. – *Anim. Behav.* 43: 519–521.
- Lima, S. L. 1990. Protective cover and the use of space: different strategies in finches. – *Oikos* 58: 151–158.
- Lima, S. L. 1998. Non-lethal effects in the ecology of predator–prey interactions. – *BioScience* 48: 25–34.
- Lima, S. L. and Dill, L. M. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. – *Can. J. Zool.* 68: 619–640.
- Lima, S. L. and Bednekoff, P. A. 1999. Temporal variation in danger drives antipredator behavior: the predation risk allocation hypothesis. – *Am. Nat.* 153: 649–659.
- Lopez de Casenave, J. 2001. Estructura gremial y organización de un ensamble de aves del desierto del Monte. – PhD thesis, Univ. de Buenos Aires, Argentina.
- Lopez de Casenave, J., Cueto, V. R. and Marone, L. 1998. Granivory in the Monte desert, Argentina: is it less intense than in other arid zones of the world? – *Global Ecol. Biogeogr.* 7: 197–204.
- Marone, L. and Horno, M. E. 1997. Seed abundance in the central Monte desert, Argentina: implications for granivory. – *J. Arid Environ.* 36: 661–670.
- Marone, L., Rossi, B. E. and Horno, M. E. 1998. Timing and spatial patterning of seed dispersal and redistribution in a South American warm desert. – *Plant Ecol.* 137: 143–150.
- Marone, L., Cueto, V. R., Milesi, F. A. and Lopez de Casenave, J. 2004. Soil seed bank composition over desert microhabitats: patterns and plausible mechanisms. – *Can. J. Bot.* 82: 1809–1816.
- Marone, L., Lopez de Casenave, J., Milesi, F. A. and Cueto, V. R. 2008. Can seed-eating birds exert top-down effects on grasses of the Monte desert? – *Oikos* 117: 611–619.
- McNamara, J. M., Green, R. F. and Olsson, O. 2006. Bayes' theorem and its applications in animal behaviour. – *Oikos* 112: 243–251.
- Meyer, M. D. and Valone, T. J. 1999. Foraging under multiple costs: the importance of predation, energetic and assessment error costs to a desert forager. – *Oikos* 87: 571–579.
- Milesi, F. A. 2006. Selección de sitios de alimentación por aves granívoras en el desierto del Monte. – PhD thesis, Univ. de Buenos Aires, Argentina.
- Milesi, F. A., Lopez de Casenave, J. and Cueto, V. R. 2008. Selection of foraging sites by desert granivorous birds: vegetation structure, seed availability, species-specific foraging tactics, and spatial scale. – *Auk* 125: 473–484.
- Mitchell, W. A. 1989. Informational constraints on optimally foraging hummingbirds. – *Oikos* 55: 145–154.
- Molokwu, M. N., Nilsson, J.-A., Ottosson, U. and Olsson, O. 2010. Seasonal variation in patch use in a tropical African environment. – *Oecologia* 164: 637–645.
- Olsson, O. and Brown, J. S. 2006. The foraging benefits of information and the penalty of ignorance. – *Oikos* 112: 260–273.
- Olsson, O. and Molokwu, M. N. 2007. On the missed opportunity cost, GUD, and estimating environmental quality. – *Israel J. Ecol. Evol.* 53: 263–278.
- Olsson, O. and Brown, J. S. 2010. Smart, smarter, smartest: foraging information states and coexistence. – *Oikos* 119: 292–303.
- Peralta, I. E. and Rossi, B. E. 1997. Guía para el reconocimiento de especies del banco de semillas de la Reserva de la Biosfera de Nacuñán (Mendoza, Argentina). – *Boletín de Extensión Científica de IADIZA* 3: 1–24.
- Petraitis, P. S. 1998. How can we compare the importance of ecological processes if we never ask, "Compared to what?" – In: Reserits, W. J. Jr and Bernardo, J. (eds), *Experimental ecology: issues and perspectives*. Oxford Univ. Press, pp. 183–201.
- Pinheiro, J. C. and Bates, D. M. 2000. Mixed-effects models in S and S-PLUS. – Springer.
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D. and the R Development Core Team 2013. nlme: linear and nonlinear mixed effects models. – <http://CRAN.R-project.org/package=nlme>.
- Polis, G. A., Wise, D. H., Hurd, S. D., Sanchez-Piñero, F., Wagner, J. D., Jackson, C. T. and Barnes, J. D. 1998. The interplay between natural history and field experimentation. – In: Reserits, W. J. Jr and Bernardo, J. (eds), *Experimental ecology: issues and perspectives*. Oxford Univ. Press, pp. 254–280.
- Price, M. V. and Reichman, O. J. 1987. Distribution of seeds in Sonoran Desert soils: implications for heteromyid rodent foraging. – *Ecology* 68: 1797–1811.
- Pulliam, H. R. and Mills, G. S. 1977. The use of space by wintering sparrows. – *Ecology* 58: 1393–1399.
- Pyke, G. H. 1984. Optimal foraging theory: a critical review. – *Annu. Rev. Ecol. Syst.* 15: 523–575.
- Repasky, R. R. 1996. Using vigilance behavior to test whether predation promotes habitat partitioning. – *Ecology* 77: 1880–1887.
- Repasky, R. R. and Schluter, D. 1994. Habitat distributions of wintering sparrows along an elevational gradient: tests of the food, predation and microhabitat structure hypothesis. – *J. Anim. Ecol.* 63: 569–582.
- Repasky, R. R. and Schluter, D. 1996. Habitat distribution of wintering sparrows: foraging success in a transplant experiment. – *Ecology* 77: 452–460.
- RStudio Team 2012. RStudio: integrated development for R. – RStudio, www.rstudio.com/.
- Scheiner, S. M. and Willig, M. R. 2011. A general theory of ecology. – In: Scheiner, S. M. and Willig, M. R. (eds), *The theory of ecology*. Univ. of Chicago Press, pp. 3–18.
- Schmidt, K. A. and Brown, J. S. 1996. Patch assessment in fox squirrels: the role of resource density, patch size, and patch boundaries. – *Am. Nat.* 147: 360–380.
- Schneider, K. J. 1984. Dominance, predation, and optimal foraging in white-throated sparrow flocks. – *Ecology* 65: 1820–1827.
- Sih, A. 1992. Prey uncertainty and the balancing of antipredator and feeding needs. – *Am. Nat.* 139: 1052–1069.
- Sih, A. 2011. Foraging theory. – In: Scheiner, S. M. and Willig, M. R. (eds), *The theory of ecology*. Univ. of Chicago Press, pp. 65–90.
- Stephens, D. W. 2007. Models of information use. – In: Stephens, D. W., Brown, J. S. and Ydenberg, R. C. (eds), *Foraging: behavior and ecology*. Univ. of Chicago Press, pp. 31–58.
- Stephens, D. W. and Krebs, J. R. 1986. *Foraging theory*. – Princeton Univ. Press.
- Stephens, D. W., Brown, J. S. and Ydenberg, R. C. (eds) 2007. *Foraging: behavior and ecology*. – Univ. of Chicago Press.
- Thompson, D. B., Brown, J. H. and Spencer, W. D. 1991. Indirect facilitation of granivorous birds by desert rodents: experimental evidence from foraging patterns. – *Ecology* 72: 852–863.
- Valone, T. J. 2006. Are animals capable of Bayesian updating? An empirical review. – *Oikos* 112: 252–259.
- Veech, J. A. 2000. Predator-mediated interactions among the seeds of desert plants. – *Oecologia* 124: 402–407.
- Veech, J. A. 2001. The foraging behavior of granivorous rodents and short-term apparent competition among seeds. – *Behav. Ecol.* 12: 467–474.
- WallisDeVries, M. F., Laca, E. A. and Demment, M. W. 1999. The importance of scale of patchiness for selectivity in grazing herbivores. – *Oecologia* 121: 355–363.
- Warton, D. I. and Hui, F. K. C. 2011. The arcsine is asinine: the analysis of proportions in ecology. – *Ecology* 92: 3–10.

- Watts, B. D. 1991. Effects of predation risk on distribution within and between habitats in Savannah sparrows. – *Ecology* 72: 1515–1519.
- Whalen, D. M. and Watts, B. D. 2000. Interspecific variation in extraction of buried seeds within an assemblage of sparrows. – *Oikos* 88: 574–584.
- Whittingham, M. J. and Markland, H. M. 2002. The influence of substrate on the functional response of an avian granivore and its implications for farmland bird conservation. – *Oecologia* 130: 637–644.
- Whittingham, M. J., Butler, S. J., Quinn, J. L. and Cresswell, W. 2004. The effect of limited visibility on vigilance behaviour and speed of predator detection: implications for the conservation of granivorous passerines. – *Oikos* 106: 377–385.
- Wiens, J. A. 1985. Vertebrate responses to environmental patchiness in arid and semiarid ecosystems. – In: Pickett, S. T. A. and White, P. S. (eds), *The ecology of natural disturbance and patch dynamics*. Academic Press, pp. 169–193.
- Williams, J. B. and Tieleman, B. I. 2001. Physiological ecology and behavior of desert birds. – In: Nolan, V. Jr and Thompson, C. F. (eds), *Current ornithology*. Volume 16. Kluwer Academics/Plenum Publishers, pp. 299–353.
- Wolf, B. 2000. Global warming and avian occupancy of hot deserts: a physiological and behavioral perspective. – *Rev. Chil. Hist. Nat.* 73: 387–392.
- Wolf, B. O. and Walsberg, G. E. 1996. Thermal effects of radiation and wind on a small bird and implications for microsite selection. – *Ecology* 77: 2228–2236.
- Wolf, B. O., Wooden, K. M. and Walsberg, G. E. 2000. Effects of complex radiative and convective environments on the thermal biology of the white-crowned sparrow (*Zonotrichia leucophrys gambelii*). – *J. Exp. Biol.* 203: 803–811.
- Ydenberg, R. C., Brown, J. S. and Stephens, D. W. 2007. Foraging: an overview. – In: Stephens, D. W., Brown, J. S. and Ydenberg, R. C. (eds), *Foraging: behavior and ecology*. Univ. of Chicago Press, pp. 1–28.
- Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A. and Smith, G. M. 2009. *Mixed effects models and extensions in ecology with R*. – Springer Science/Business Media.