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Food abundance determines distribution and density of a frugivorous bird across seasons

Lisa H. Crampton, William S. Longland, Dennis D. Murphy and James S. Sedinger

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Although food abundance is a principal determinant of distribution and abundance of many animals, most previous studies have not quantitatively assessed its importance relative to other factors that may also determine species distributions. We estimated frugivorous phainopepla *Phainopepla nitens* occupancy and density, food density, and vegetation structure on transects in fragmented mesquite and acacia woodlands over three years in non-breeding and breeding seasons. Using an AIC framework and controlling for detection probability, we determined relative impacts of food abundance, vegetation structure, and habitat fragmentation on patch occupancy and density, and concomitant extinction and colonization probabilities of phainopeplas. Initial occupancy in winter 2002 was high (0.87 ± 0.047), and primarily positively correlated with food abundance and woodland area (Akaike weights $w_i = 0.998$ and 0.750 respectively). Woodland area more strongly influenced occupancy where food was scarcer. Phainopepla density in both seasons was strongly positively correlated with food abundance, especially in the 2002 drought when density was higher ($w_i = 1.0$ for food and year). Density was higher in acacia than mesquite woodlands ($w_i = 1.0$), and moderately negatively correlated with elevation ($w_i = 0.789$). Extinction probability (patches vacated) was low (0.078 ± 0.040), and principally influenced by phainopepla density ($w_i = 0.968$) and tree height ($w_i = 0.749$). Colonization probability was low (0.15 ± 0.034) and determined by vegetation structure ($w_i = 1.0$). Much recorded colonization was reoccupancy of woodlands previously occupied by single males in winter, then vacated in a breeding season. These results suggest that for an animal occupying a highly fragmented landscape, distributions and densities at the habitat patch scale are driven by food abundance, are moderately affected by habitat fragmentation, and are slightly influenced by vegetation structure.

Ecologists have long appreciated that food availability strongly influences animal distribution and abundance, as illustrated by the optimal foraging and habitat selection literatures (Charnov 1976, White 2008). In simplified models, foragers closely track food resources across patches, and choose patch(es) that maximize fitness, resulting in an ideal, free distribution of individuals that mirrors food distribution (Fretwell and Lucas 1970). Several empirical studies have demonstrated that animals occur more frequently or in greater numbers in habitat patches with more abundant food, and for some animals food abundance is the key determinant of distribution (Rey 1995, Haythornthwaite 2005, van Gils et al. 2006). However, the correlation between food and distribution of other animals is weakened by diverse factors, such as predation, social interactions, climate, or attempts to forecast future conditions (Marra 2000, Telleria and Perez-Tris 2007).

Some of these factors, such as climate and predation, may be alleviated by physical attributes of the environment, such as vegetation height, density, and cover; hence, vegetation

structure also can influence animal distribution and abundance. Indeed, vegetation structure has been considered the principal influence on nesting bird distribution, because it mitigates nest predation risk (Martin 1993, Doran and Holmes 2005); but as with food availability, sometimes no clear correlation between vegetation structure and breeding distribution emerges (Nagy and Holmes 2004, Telleria and Perez-Tris 2007). Furthermore, landscape-level processes such as habitat fragmentation can affect habitat quality and thus animal distribution and abundance. Occupancy rates and abundances are sometimes lower in small or isolated patches, perhaps due to harsher microclimates, increased predation, or lower availability of territories or mates (Murcia 1995, Burke and Nol 2000, Chalfoun et al. 2002). However, this trend does not hold for all species or fragmented landscapes (Schmiegelow et al. 1997, Dardanelli et al. 2006). Therefore, to assess determinants of distribution and abundance in fragmented landscapes, multiple factors at diverse spatial and temporal scales should be considered simultaneously. Until recently, however, most

pertinent studies considered food abundance, vegetation structure, and habitat fragmentation independently, and many that examined multiple factors (Doran and Holmes 2005, Cameron and Cunningham 2006) did not employ multiple factor statistical analyses to assess relative importance of individual factors (but see Burke and Nol 2000, Oliver et al. 2003, Karpanty et al. 2006).

A key difficulty in such studies is quantifying food abundance and availability. This problem can be overcome substantively by studying frugivores whose primary food resources are typically conspicuous and easy to quantify, and who often track variation in fruit abundance across space and time (Rey 1995, Worman and Chapman 2006). Phainopeplas *Phainopepla nitens*, frugivorous birds of the southwestern United States and Mexico, are ideal candidates for investigating effects of food abundance on distribution and abundance. Phainopeplas overwinter and breed in simple, but highly fragmented, desert woodlands dominated by a few species of trees, thus facilitating interseasonal comparisons of distribution and abundance. During their entire desert residency (both winter and breeding periods), phainopeplas consume nearly exclusively

berries of desert mistletoe *Phoradendron californicum*, and like some Australian mistletoe specialists, track temporal and local spatial variation in berry abundance (Anderson and Ohmart 1978, Watson 1997, Oliver et al. 2003). The typical dependence of primary productivity, and thus food availability, on local weather patterns discussed by White (2008) is particularly strong in the arid North American deserts where phainopeplas occur (Beauley 1974).

We assessed relative roles of food abundance, vegetation structure, and habitat fragmentation in determining distribution and density of phainopeplas in non-breeding and breeding seasons in mesquite *Prosopis* spp. and acacia *Acacia greggii* woodlands in the northeastern Mojave Desert, the coldest and driest part of their range (Fig. 1). In this region, woodlands vary greatly in area, extent of anthropogenic fragmentation, mistletoe abundance, and vegetation structure, providing a gradient in each parameter. We considered the two seasons separately, because the relative influence of these factors may differ between seasons. We tested three non-exclusive hypotheses. Because phainopeplas' diet consists mainly of mistletoe berries during both seasons (Walsberg 1977), we hypothesized that their distribution

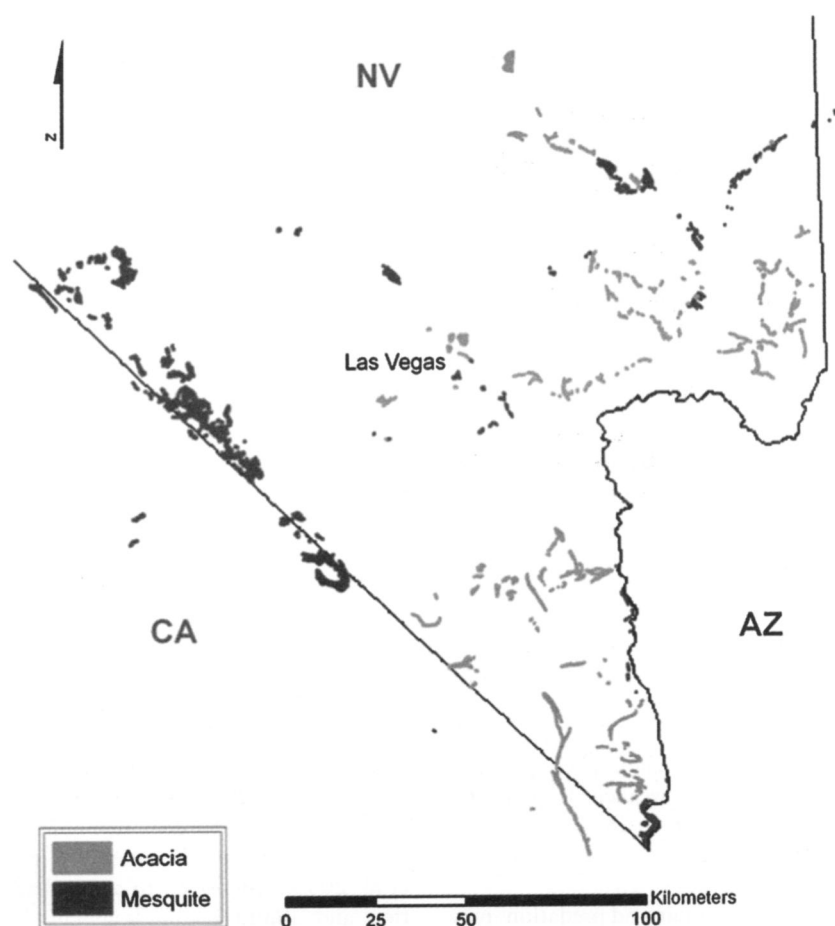


Figure 1. Distribution of mesquite and acacia woodlands in the northeastern Mojave Desert (southeastern California, southern Nevada and northwestern Arizona). Study sites were distributed throughout these woodlands.

and density should be positively correlated with temporal and spatial variation in food abundance. We predicted that berry abundance should be the most important determinant of bird distribution and density in both seasons, and that woodland patches with very little mistletoe would not constitute phainopepla habitat. Second, we hypothesized that vegetation structure and habitat fragmentation should influence phainopepla distribution and density to a lesser degree, but thus phainopeplas would not solely track food abundance. We predicted that vegetation structure would be more important in the breeding season when birds need to mitigate nest predation and microclimate than in winter, when acquiring sufficient food is essential to both winter survival and subsequent breeding attempts (Studds and Marra 2005). Finally, we predicted that phainopepla distribution and density should be positively correlated with woodland area, and negatively correlated with woodland isolation, as phainopeplas possess some qualities typical of area-sensitive species (Dardanelli et al. 2006). This study has significant conservation relevance, as phainopepla population declines and extirpations have been attributed to fragmentation and loss of desert woodland habitats (Chu and Walsberg 1999).

Material and methods

Study species, area and sites

The phainopepla is a medium-sized songbird endemic to southwestern North America with an unusual life history. It occupies the region's deserts from early fall to late spring, and migrates to coastal and more mesic areas during the summer; remarkably, breeding occurs among a majority of individuals in both parts of the range (Chu and Walsberg 1999). Both sexes establish territories in desert woodlands in mid-fall, and most individuals hold the same territories in non-breeding and spring breeding (February – June) seasons (Chu and Walsberg 1999, Crampton unpubl.). Their desert residency coincides with mistletoe fruit production, which comprises most of the diet of both adult and nestling phainopepla, even during the breeding season (Walsberg 1977). Fruiting is usually spatially synchronous across the landscape, beginning in early fall, peaking in December – January, and declining through spoilage and consumption until June (Walsberg 1977); in our study area berry abundance declined by ~450 berries per day between late fall and mid-spring (Crampton unpubl.). Thus when establishing territories, phainopeplas must predict food abundance several months ahead. Failure of mistletoe berry crops due to hard frosts or extreme drought results in mass Phainopepla migrations to woodlands that still have berries (Chu and Walsberg 1999). Previous work on phainopeplas has focused on individual-level questions such as diet, digestion, energetics and social behavior (Walsberg 1975, 1977, Krueger 1998, Chu and Walsberg 1999); this study is the first to examine extensive population-level questions across multiple sites at the landscape scale, and complements others we have conducted that examined nest selection and survival (Crampton 2004).

This study was conducted in the northeastern Mojave Desert of southern Nevada, southeastern California and northwestern Arizona. Las Vegas, NV, at 36°10'N and

115°10'W, lies at the approximate center of the study area (Fig. 1). Winter temperatures (30-year mean Jan maximum/minimum = 13.9°C/2.7°C) are lower in this periphery of phainopeplas' range than in the rest of the range. Mean annual precipitation is 11.4 cm, but a severe drought occurred from early 2000 – 2003. The second year of the study, 2002, was especially dry; total annual rainfall was 3.7 cm, and only 0.3 cm fell in the breeding season (NOAA 2004).

In this region, only three host species for desert mistletoe occur: honey mesquite *Prosopis glandulosa*, screwbean mesquite *P. pubescens*, and catclaw acacia *Acacia greggii*. These species form woodlands dominated by one or both mesquites ('mesquite' type), or by acacia ('acacia' type), which differ in mistletoe abundance and vegetation structure (e.g. tree height and tree density); for example, mesquites often grow > 4 m tall, whereas acacias rarely reach 4 m. All are restricted to areas with available groundwater, so variably-sized woodland patches occur in somewhat aggregated clusters, which in turn are widely separated in a landscape dominated by Mojave scrub (Fig. 1). Such clustering might lead to spatial autocorrelation in both predictor and response variables; however, all these variables varied greatly within these clusters, so we contend that for the time scales of this study, there is little reason for concern about autocorrelation.

To locate as many mesquite and acacia woodlands as possible in our study area, we used a) a GIS coverage of 45 woodlands that had been generated by local land managers in the late 1990s, and b) ground reconnaissance during the pilot season (October 2000 to June 2001), which added 22 woodlands to our GIS database. We conservatively defined a woodland as a continuous stand of mesquite or acacia. We considered woodlands distinct if separated by ≥ 30 m, the mean radius of phainopepla territories (Walsberg 1977), because it is easier to combine smaller woodlands into larger ones than to separate larger woodlands, if necessary for post-hoc analyses in GIS. Furthermore, the analytical tool we used to assess isolation of woodlands incorporated the distance and size of nearby woodlands. Woodlands ranged from 0.1 – 2500 ha in area; we surveyed woodlands encompassing this entire range.

We did not survey entire woodlands, but established smaller study sites by randomly generating UTM coordinates in the GIS coverage. The number of sites per woodland was proportional to woodland area, thus some woodlands contained multiple sites (one site per 300 ha of woodland). In the pilot study season, October 2000 – June 2001 (hereafter 2001), we sampled 72 sites in 45 woodlands at least once. In the two full field seasons (November 2001 – June 2002, called 2002; and January – June 2003, called 2003), we sampled 76 random study sites \geq four times in each field season. We retained 44 pilot study sites, but excluded some pilot sites in woodlands in which there was > 1 site per 300 ha. Also, we sampled five remote sites infrequently (\leq twice) in 2002; two of these were sampled twice in 2003. In total, we surveyed 103 sites at least once in three years; 44 of these were surveyed in all three years, and 76 surveyed in two years (Appendix 1). We estimate that we surveyed ~80% of woodlands, encompassing the range of woodland conditions in terms of vegetation structure, food abundance, and landscape metrics in the study area, including some sites devoid of mistletoe.

Bird occupancy and density surveys

To assess occupancy dynamics (that is, initial occupancy, colonization and extinction of patches) and density, at each study site we surveyed phainopeplas using the line transect method of Bibby et al. (1992) along a randomly established 500-m-long transect within the woodland. We recorded sex, age and approximate perpendicular distance from transects (to the nearest 5 m up to 30 m away from the transect and to the nearest 10 m thereafter) for each individual detected. We surveyed in two 'seasons': non-breeding (mid-November to early February) and breeding (defined by the date on which the first nest was found). In 2001, most transects were sampled once during the breeding season. In 2002 and 2003 most transects were surveyed two-three times/season, but a few transects that had little (<100 berries) mistletoe were surveyed only once/season; the latter were included for descriptive purposes and not analyses.

To estimate densities where phainopepla were detected, we generated detection functions (i.e. the probability of detecting a phainopepla given its distance from the transect) for each woodland type (mesquite vs acacia) \times year \times survey visit combination in program DISTANCE (Thomas et al. 2004). As recommended by Buckland et al. (2001), we truncated the largest 5% of observation distances used in DISTANCE, which was 70 – 100 m, depending on the detection function. For woodlands with multiple sites, we averaged data across sites. We calculated weighted mean density/woodland from two estimates for each season. For woodlands narrower than the maximum distance used in the detection function, we divided the maximum detection function distance by half the width of the woodland to obtain a density adjustment factor. We multiplied weighted mean density by this factor to produce an adjusted density.

Vegetation surveys and estimation of resource abundance

Focal trees (2001)

At 43 sites in 2001, the pilot year, we used a T² sampling method to locate the nearest mistletoe-infected tree (tree A) from each of eight random points, and the nearest infected tree (tree B) to A (Krebs 1989). If there was no tree within a 30-m radius of the point or A, no measurements were made. This method allowed accurate estimation of proportion ('incidence') and density of infected trees, and identification of focal trees for estimates of mistletoe production, but was too labor-intensive for subsequent years. On each tree, we counted numbers of mistletoe plants with and without berries in March and April.

Vegetation transects (2002-2003)

In 2002, we established two 100 \times 20 m belt transects parallel to and within areas surveyed during bird transects (Anderson and Ohmart 1978). To sample vegetation in the area surveyed, each belt transect was located a random distance from the bird transect and began at a random distance along the bird transect. In 2002, we counted all trees or shrubs > 1 m in height in belt transects, and recorded species, mistletoe infection status (infected or not), and height

in 1-m categories. In 2003, we estimated canopy area of trees in belt transects by pacing out length and width of the canopy and applying the formula for the area of an ellipse. We also estimated proportion of each transect covered by shrubs and trees (% cover). We took the mean of each variable across all trees in both belt transects. For woodlands with several sites, we calculated the mean of each variable across all transects in all sites.

In November – December 2001, March 2002 and 2003, we estimated the number of berries on each mistletoe on each tree as follows. Up to 100 berries were counted per plant; if there were more berries, the number of groups/mistletoe plant containing 100 berries was estimated. For plants estimated to have >2000 berries, we estimated numbers of groups containing 500 berries. We then categorized the number of berries/tree as: 0 berries; <10; <50; <100; <500; <1000; <5000; <10 000; <15 000; <20 000 berries etc. To test this method, we compared independent estimates made by six trained observers; estimates were always in the same category. We used the maximum number in March for each category in analyses, assuming that berries had been eaten during the study period. This metric represents minimum winter berry abundance and maximum spring berry abundance. The Pearson correlation between berry abundance in winter 2001/2002 and March 2002, and the Spearman correlation between rank abundance in those seasons were both high ($r^2 = 0.72$ and $\rho = 0.74$), thus relative berry abundance in a site did not vary substantially between seasons. Total maximum berry density was summed across all infected trees in both belt transects. For woodlands with more than one site, we calculated mean berry density across all sites.

Habitat fragmentation metrics (woodland area and isolation)

We ran program FRAGSTATS (McGarigal et al. 2002) on the mesquite-acacia GIS coverage to generate a measure of isolation of each woodland, 'proximity', which was based on area and nearest distance of all woodlands within a 500-m [the longest distance phainopeplas traveled during repeat 20-min focal observations of 16 pairs (Crampton unpubl.)] radius of each woodland. Proximity thus incorporates both woodland isolation and fragmentation (McGarigal and Marks 1995). Indices based on larger search radii (1 km, 5 km and 10 km) were also evaluated, but they did not differ from the 500-m index in their influence on phainopepla distribution and density. We calculated woodland area from the GIS coverage.

Statistical analyses

Prior to statistical analysis, we standardized ((observation-mean)/standard deviation) all continuous covariates to have mean = 0 and standard deviation = 1. Thus they had similar ranges of values, and their β coefficients could be compared directly.

Occupancy of phainopeplas in 2001 (pilot season)

For 2001, we modeled woodland occupancy against food abundance, incidence of infection, woodland area, and proximity using multiple logistic regression (PROC LOGISTIC,

SAS 2005). We used proportion of trees containing fruiting mistletoe as our metric of food abundance. We considered woodlands occupied if phainopeplas were present on ≥ 1 visits during the breeding season (late February or March – end of April). We multiplied the covariance matrix by deviance/DF to correct for overdispersion (SAS 2005), and assessed goodness-of-fit with the Hosmer–Lemeshow (2003) test. The significance level was $\alpha = 0.05$; we report both significant and marginally non-significant ($p < 0.1$) results. We did not have sufficient data to assess predictors of phainopepla density in 2001, nor to run the occupancy models used for 2002 and 2003 data.

Occupancy and density in 2002 and 2003

For 2002 and 2003 data, we used an information theoretic approach to evaluate predictors of occupancy in Program PRESENCE (Hines 2006) and density in ANCOVA in PROC MIXED (SAS 2005). For each response variable, we explicitly considered temporal variation. Because we had multiple visits to sites within and among seasons, we were able to use the multiseason feature in Program PRESENCE to control for detection probability while modeling initial occupancy in winter 2002 and subsequent changes in occupancy status of sites between seasons and years (i.e. colonization and extinction of patches). Analogous to a robust design in mark-recapture studies, explicitly modeling these ‘occupancy dynamics’ in PRESENCE’s multiseason feature was preferable to modeling single-season occupancy over several subsequent seasons because the former accounted for temporal autocorrelation and the latter had more restrictive assumptions (MacKenzie et al. 2006). Furthermore, PRESENCE includes temporal and environmental differences in detection probability when estimating occupancy, colonization, and extinction probabilities.

We used Akaike’s information criteria (adjusted for small sample sizes, AICc, Burnham and Anderson 2002) to assess weight of evidence for models representing our a priori predictions regarding the roles of food abundance, vegetation structure and habitat fragmentation as predictors of occupancy dynamics and density:

- 1) Vegetation structure: probability of occupancy and colonization, and density should be greater, and probability of extinction lower, in woodlands with tall trees, high % cover, and many trees, given phainopepla nest site preferences (Crampton 2004).
- 2) Food resources: probability of occupancy and colonization, and density should be greater, and probability of extinction lower, in woodlands and years with more mistletoe berries.
- 3) Habitat fragmentation: probability of occupancy and colonization, and density should be greater, and probability of extinction lower, in larger, less isolated woodlands.
- 4) Combinations and relative importance of variables: For all dependent variables, models combining vegetation structure, food, and fragmentation variables should have more support than models with only one type of variable. However, food abundance should have greater influence on occupancy parameters than other variables.

Prior to modeling, we used techniques described in Hosmer and Lemeshow (2003) to reduce the number of predictor variables. We identified a set of standardized variables that represented vegetation structure, food resources, and habitat fragmentation metrics, and that were not highly correlated (pairwise correlations less than $r = 0.4$, and typically less than $r = 0.2$). Next, we ran simple (univariate) logistic or linear regression (SAS 2005) on remaining variables. We retained those variables that predicted phainopepla distribution or density with $p < 0.25$ and two variables for which we had specific hypotheses (tree height and proximity) for inclusion in models (Hosmer and Lemeshow 2003). In the final variable set, pairwise correlations between variables that represented the different key hypotheses (e.g. berry abundance vs vegetation structure or habitat fragmentation variables) all had $r < 0.25$. This set of variables also contained some ‘nuisance’ covariates for which we did not have specific hypotheses, for example elevation and woodland type. We log-transformed berry density because its distribution was strongly left-skewed.

Using the multi-season feature in Program PRESENCE, we simultaneously estimated detection probability, initial probability of occupancy in winter 2002, and probability of colonization and local extinction of woodlands in spring 2002, winter 2003 and spring 2003 as functions of our predictor variables (Hines 2006, MacKenzie et al. 2006). In PRESENCE, each season was a ‘primary’ occasion, and each visit within seasons was a ‘secondary’ occasion. The secondary occasions were used to estimate detection probability for each primary occasion, while simultaneously estimating occupancy dynamics between primary occasions (seasons). We included three secondary occasions for all primary occasions except non-breeding 2003 (two secondary occasions). We modeled occupancy at 60 woodlands, 180 colonization–extinction events (three primary occasions \times 60 woodlands), and detection over four primary occasions at each woodland.

To assess our hypotheses regarding occupancy dynamics, in PRESENCE we first developed base models to control for different combinations of the nuisance covariates year, season and woodland type. Models with time-varying (seasonal or annual) occupancy, colonization, or extinction did not converge, and with woodland type on its own had little support. Thus the base model was the intercept-only model for occupancy, colonization and extinction. For detection probability, the base model was season (non-breeding vs breeding) + woodland type.

Next, we considered models with all possible single variable and pairwise combinations of food, structure, and fragmentation covariates for one parameter (occupancy, colonization, or extinction), while holding the covariate structure of the other parameters constant (models with $>$ three covariates/parameter did not perform well). For detection probability, we held covariate structure for the other parameters constant, and ran models containing each covariate individually or with all covariates minus the covariate of interest. We modeled the effect of food abundance in a time variant matrix, so that each year’s food abundance was applied to extinction and colonization probabilities for that year. We controlled for two nuisance variables: 2002 winter phainopepla density on extinction probability (time-variant models for phainopepla density did not converge

and density patterns did not differ significantly within sites, Results), and elevation on all parameters.

This stepwise approach ensured that all covariates were considered in equal numbers of models, allowing assessment of the relative importance of each. To do so, we a) model averaged over all models with weight > 0.01 to determine the average beta coefficient and standard error for each variable, and b) summed the weights of all models with weights > 0.01 containing that variable to assess relative variable importance (Burnham and Anderson 2002).

To assess hypotheses regarding predictors of density, we used a similar model-building approach in repeated measures analysis of covariance in PROC MIXED (SAS 2005). We included woodland as a repeated measure, since the same woodlands were sampled each year and season, and specified the compound symmetry (cs) variance-covariance matrix. We normalized bird density with a square root transformation. As in PRESENCE, we started by building a base model from various combinations of year and woodland type; the year + woodland type base model had more support than other models. Building on the base model, we then ran models predicting density that included all covariates in 1) each 'group' (structure, food, or fragmentation), 2) all pairs of groups, and 3) all three groups (the 'full' model). Also, we ran models with all covariates except the covariate of interest. Since all variables were included in equal numbers of models, we model averaged and calculated relative variable importance as described above.

Results

Predictors of bird distribution among woodlands

Occupancy primarily was determined by food abundance, followed by habitat fragmentation, and was not influenced by vegetation structure. In spring 2001, occupancy was significantly positively correlated only with food abundance (i.e. proportion of trees with berries: $\beta = 1.92 \pm 0.59$, Wald $\chi^2 = 10.63$, $p = 0.0011$, $n = 21$ occupied, 14 unoccupied woodlands), not fragmentation. In 2002 probability of initial occupancy modeled in PRESENCE, which was very high (40/60 woodlands had $\geq 97\%$ chance of occupancy; range: 0.36 – 1.0), was positively correlated with both food abundance and woodland area. All top models contained food abundance, and ~75% of models contained area (Table 1, 2, Fig. 2). Woodland area more strongly influenced probability of occupancy where food abundance was below mean berry density (43 055 \pm 16 696 berries; Fig. 2). Threshold berry density at which probability of occupancy changed from 0 to 1 was higher for small versus large woodlands (Fig. 2, 3). For example, in a 0.5 ha woodland, probability of occupancy reached 1.0 at 1500 berries ha⁻¹, whereas it reached 1.0 at 400 berries ha⁻¹ in a 2500 ha woodland.

In contrast, both probabilities of colonization and extinction (i.e. probability of change in occupancy status between seasons) were predicted by vegetation structure, not by food abundance or habitat fragmentation. Because so many woodlands were occupied, and extinction probabilities were low (< 0.5), colonization probabilities in most woodlands also were low (159/180 events had < 0.03 probability of colonization,

Table 1. Results of Program PRESENCE models, evaluating factors influencing initial occupancy in winter 2002 (Ψ), colonization (γ), extinction (ϵ), and detection probability (p) of phainopeplas in desert woodlands in 2002–2003. Included are models with AICc weights $w_i > 0.01$. Factors include food density in 2002 (food02), phainopepla density in winter 2002 (PHAI density), woodland area (area, in ha), tree height (tree ht, in m), %cover, elevation (elev, in m), winter versus breeding season (WS), woodland type (wdl type), and proximity (prox). K = no. of factors + intercept. n = 60 sites for Ψ , 180 sites \times intervals between primary periods for ϵ and γ , and 240 sites \times primary periods for p .

Model	K	AICc	Δ AIC	w_i
Ψ (food02, area), γ (tree ht, % cover), ϵ (tree ht, PHAI density), p (WS, wdl type, prox, area, tree ht, % cover)	16	582.77	0	0.4749
Ψ (food02, prox), γ (tree ht, % cover), ϵ (tree ht, PHAI density), p (WS, wdl type, prox, area, tree ht, % cover)	16	586.1	3.33	0.0898
Ψ (food02, tree ht), γ (tree ht, % cover), ϵ (tree ht, PHAI density), p (WS, wdl type, prox, area, tree ht, % cover)	16	586.35	3.58	0.0793
Ψ (food02, elev), γ (tree ht, % cover), ϵ (tree ht, PHAI density), p (WS, wdl type, prox, area, tree ht, % cover)	16	586.45	3.68	0.0754
Ψ (food02, area), γ (tree ht, % cover), ϵ (PHAI density), p (WS, wdl type, prox, area, tree ht, % cover)	15	586.62	3.85	0.0693
Ψ (food02, area), γ (tree ht, % cover), ϵ (area, PHAI density), p (WS, wdl type, prox, area, tree ht, % cover)	16	587.58	4.81	0.0429
Ψ (food02, area), γ (tree ht, % cover), ϵ (% cover, PHAI density), p (WS, wdl type, prox, area, tree ht, % cover)	16	587.59	4.82	0.0427
Ψ (food02, area), γ (tree ht, % cover), ϵ (prox, PHAI density), p (WS, wdl type, prox, area, tree ht, % cover)	16	587.73	4.96	0.0398
Ψ (food02, area), γ (tree ht, % cover), ϵ (elev, PHAI density), p (WS, wdl type, prox, area, tree ht, % cover)	16	588.6	5.83	0.0257
Ψ (food02, area), γ (tree ht, % cover), ϵ (wdl type, PHAI density), p (WS, wdl type, prox, area, tree ht, % cover)	16	588.62	5.85	0.0255
Ψ (food02, area), γ (tree ht, % cover), ϵ (tree ht, % cover), p (WS, wdl type, prox, area, tree ht, % cover)	16	590.34	7.57	0.0108

and 168/180 events had < 0.17 probability of extinction); however, colonization probabilities were ≥ 0.9 for 12 events. Colonization and extinction were negatively correlated with % cover and phainopepla density, respectively, and were both positively correlated with tree height (Table 2). Although food and fragmentation had no significant influence, many colonization/extinction events occurred when the same six small (< 20 ha) and/or berry-poor (< 500 berries ha⁻¹) mesquite woodlands changed occupancy status between seasons. Remaining sites were only occupied once or in one year of the study (Table 5). At all but two patches with high extinction probabilities only a single male was detected.

Predictors of bird density

Like occupancy, bird density was principally determined by food abundance; however, neither fragmentation nor

Table 2. Model averaged β estimates (\pm SE), and relative importance (0 = no evidence, 1 = strong evidence) of individual variables influencing occupancy (in winter 2002), colonization, and extinction of desert woodlands used by phainopeplas in 2002 and 2003. Model averaging was conducted over models with weights > 0.01 . Relative variable importance (RVI) is based on the sum of the weights of all models containing a given variable with weights > 0.00 . All variables were included in equal numbers of models.

Variable	Occupancy		Colonization		Extinction	
	$\beta \pm$ SE	RVI	$\beta \pm$ SE	RVI	$\beta \pm$ SE	RVI
2002 food abundance (berries ha ⁻¹)	160 \pm 7.4	0.998				0.002 ^a
2002 phainopepla density (birds ha ⁻¹)					-2.4 \pm 1.3	0.968
Tree height (m)	0.015 \pm 0.049	0.080	19.6 \pm 8.0	1.000	0.69 \pm 0.28	0.749
% cover		0.001 ^a	-22.6 \pm 10.9	1.000	0.016 \pm 0.024	0.060
Woodland area (ha)	7.46 \pm 5.36	0.750			-0.020 \pm 0.027	0.044
Proximity	0.030 \pm 0.052	0.090			-0.019 \pm 0.027	0.043
Elevation (m)	-0.001 \pm 0.04	0.076			-0.002 \pm 0.011	0.035
Woodland type (Mesquite)					0.000 \pm 0.024	0.026

^ano models with weights > 0.01 contained these variables.

vegetation structure had strong influence. All top models of density contained food abundance and a strong food \times year interaction (Table 3, 4). Food abundance influenced density more in 2002, when food was scarcer and mean density was significantly higher (1.2 ± 0.06 phainopeplas ha⁻¹), than 2003 (0.97 ± 0.06 ha⁻¹; Table 4, Fig. 4). Density ranged from 0.01 – 6.48 phainopeplas ha⁻¹ in the 2002 non-breeding season, and 0.04 – 8.14 ha⁻¹ in the 2002 breeding season; and 0.04 – 5.01 ha⁻¹ in the 2003 non-breeding season, and 0.11 – 4.75 ha⁻¹ in the 2003 breeding season. Each season, 33 sites supported < 2 phainopeplas ha⁻¹. Density did not differ significantly between seasons. Bird density did differ among sites ($Z_{177} = 3.76$, $p < 0.0001$), but since sites had similar relative densities across years (repeatability $T = 0.7$, Hayes and Jenkins 1997), the between-year difference in overall density was primarily due to density increases in high-density sites in 2002.

Two 'nuisance' covariates also influenced bird density. Elevation also appeared in most density models, including the best supported model, and was negatively correlated with bird density. Woodland type occurred in all top models, including those with most or all covariates, suggesting that for reasons not captured by those covariates, density was

higher in acacia (1.2 ± 0.08 phainopeplas ha⁻¹) than mesquite (0.94 ± 0.07 phainopeplas ha⁻¹) woodlands.

Discussion

By surveying many woodlands encompassing gradients of habitat fragmentation, vegetation structure, and food abundance, and controlling for detection probability, we established the primacy of food abundance, followed by habitat fragmentation, in determining occupancy and density of a dietary specialist that uses the same fragmented woodlands in both breeding and non-breeding seasons. In contrast, vegetation structure played only a minor role in predicting distribution and density, affecting only the very low colonization and extinction probabilities (i.e. the rare seasonal changes in occupancy status). Food resources were especially important in explaining distribution and density in a drought year, and in small patches. Furthermore, extinction probability was strongly negatively correlated with phainopepla density; the presence of single males combined with the small size and/or scarce food resources of these patches suggests they were marginal in quality. While density measures do not directly

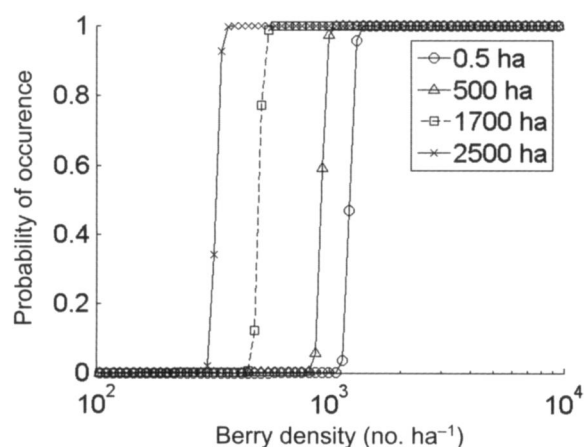


Figure 2. Relationship between food abundance (mistletoe berry density) and probability of initial phainopepla occupancy of woodlands of different sizes in the northeastern Mojave Desert (winter 2002).

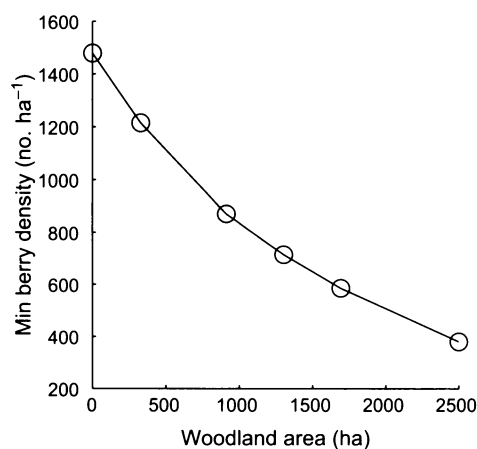


Figure 3. Minimum food abundance (mistletoe berry density) required for probability of phainopepla occupancy to be > 0.999 , in woodlands of different sizes in the northeastern Mojave Desert (winter 2002).

Table 3. Results of PROC MIXED models used to compare predictors of phainopepla density in occupied desert woodlands, 2002–2003. Included are models with AICc weights, $w_i > 0.01$. For descriptions of variable abbreviations see Table 1. K = no. of factors + intercept. n = 177 sites \times seasons sampled.

Model	K	AICc	Δ AICc	w_i
year, wdl type, food, year \times food, elevation	8	186.9	0	0.5855
year, wdl type, food, year \times food	7	189.8	2.9	0.1373
year, wdl type, food, year \times food, tree ht, %cover, no. of hosts	10	191.5	4.6	0.0587
all but hosts: year, wdl type, food, year \times food, tree ht, %cover, area, proximity, elevation	13	191.8	4.9	0.0505
all but area: year, wdl type, food, year \times food, tree ht, %cover, no. of hosts, proximity, elevation	13	191.9	5	0.0481
all but tree ht: year, wdl type, food, year \times food, no. of hosts, %cover, area, proximity, elevation	13	192.3	5.4	0.0393
all but proximity: year, wdl type, food, year \times food, tree ht, %cover, no. of hosts, area, elevation	13	192.6	5.7	0.0339
all: year, wdl type, food, year \times food, tree ht, %cover, no. of hosts, area, proximity, elevation	14	194.1	7.2	0.016
year, wdl type, food, year \times food, area, proximity	10	194.2	7.3	0.0152

elucidate underlying population parameters or individual patch quality (Van Horne 1983, Temple and Wiens 1989), exploring variation in density across numerous patches of differing quality enhances its utility as a means of understanding those population processes.

Like some Australian mistletoe specialists, a positive correlation between levels of mistletoe infection, but not specifically berries, and phainopepla abundance within patches has been observed near the core of the species' range (Anderson and Ohmart 1978, Watson 1997, Oliver et al. 2003). However, this is the first study to quantify this correlation across patches. The strong influence of food is in general agreement with two studies that found that distribution and

Table 4. Model averaged β estimates (\pm SE), and relative importance (0 = no evidence, 1 = strong evidence) of individual variables influencing phainopepla density in occupied desert woodlands, 2002–2003. Model averaging was conducted over models with weights > 0.01 . Relative variable importance (RVI) was based on the sum of the weights of all models containing a given variable with weights > 0.0 . All variables were included in equal numbers of models.

Variable	$\beta \pm$ SE	RVI
Year (2002)	0.177 \pm 0.0558	1.0000
Woodland type (<i>Acacia</i>)	0.294 \pm 0.116	1.0000
Food density	0.0341 \pm 0.0671	0.99995
Year \times food density	0.2647 \pm 0.0771	0.99974
Tree height (m)	-0.00703 \pm 0.0141	0.2228
No. of hosts	-0.00361 \pm 0.0117	0.21163
% cover	0.0291 \pm 0.0147	0.25418
Elevation (m)	-0.0954 \pm 0.0429	0.7888
Woodland area (ha)	0.00268 \pm 0.00756	0.17061
Proximity	0.00723 \pm 0.00921	0.1848

Table 5. Seasonal and annual patterns of detections of phainopeplas in mesquite and acacia woodlands in the northeastern Mojave Desert, 2002–2003. Numbers represent numbers of woodlands. Phainopeplas were not detected in either year in four woodlands.

Year	Only detected that year	Not detected that year	Detected in both seasons	Detected in non-breeding season only	Detected in breeding season only
2002	5	8	29	9	3
2003	2	7	30	8	5

abundance of several frugivorous species was correlated with experimentally manipulated fruit abundance (Moegenburg and Levey 2003, Borgmann et al. 2004). The weak negative correlation between woodland elevation and phainopepla density also may reflect spatial variation in food abundance, perhaps due to warmer temperatures and higher mistletoe infection rates at lower elevations (Aukema 2004).

In our study, as in many others of woodland and forest birds, patch area was moderately positively correlated with occupancy (Doherty and Grubb 2000, Watson et al. 2005). Smaller patches are less likely to be occupied due to unfavorable microclimates, elevated nest parasitism and predation rates, and lack of mates (Murcia 1995, Burke and Nol 2000, Chalfoun et al. 2002). Indeed, phainopepla nest survival was lower in small patches, and predation was the primary cause of nest failure (Crampton 2004). Also, forest bird species dependent on scarce or unusual resources, like phainopeplas, typically only occupy large fragments (Telleria and Santos 1995, Zanette 2000). Abiotic conditions in small patches may also indirectly affect birds if they negatively influence food resources or vegetation structure, but in our study and that of Rodewald and Vitz (2005), patch area was not strongly correlated with food abundance or vegetation structure metrics. Perhaps those large patches with lower food density allowed phainopeplas to compensate by occupying larger or shifting territories. This may be analogous to Australian frugivores' dependence on close-proximity networks of patches of fruit trees (Price et al. 1999). Larger or shifting territories also might explain the poor correlation between woodland area and phainopepla

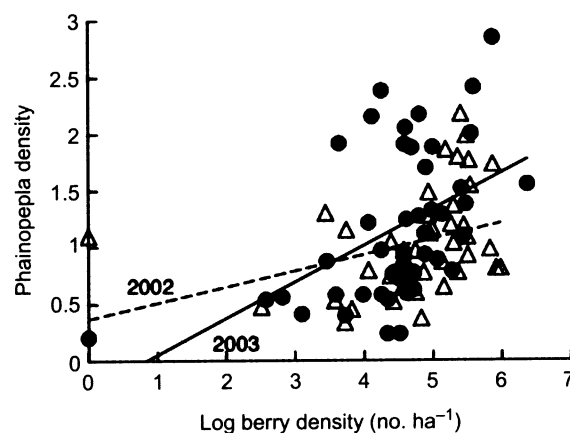


Figure 4. Relationships between food abundance (mistletoe berry density) and phainopepla density in the northeastern Mojave Desert, in drought (2002: dots, solid line) and normal (2003: triangles, dashed line) years.

density, which contradicts a model predicting that birds nesting and foraging exclusively within a habitat patch (as do phainopeplas) should reach higher densities in larger patches (Estades 2001). To dietary specialists, large woodland patches with little food may be less attractive than large patches with abundant food, and perhaps even less suitable than small patches with abundant food.

Remarkably, vegetation structure, usually considered the best predictor of nest predation risk and microclimate and thus to be more important than food abundance in predicting bird distributions, did not appreciably influence phainopepla occupancy and density, even in the breeding season (Martin 1993, Oliver et al. 2003, Cameron and Cunningham 2006). In this respect, phainopeplas differ from another mistletoe specialist, the painted honeyeater, which selected woodlands for both mistletoe and vegetation structure (Oliver et al. 2003), and from frugivorous blackcaps that purportedly did not perfectly track food abundance in the non-breeding season because they selected habitat features that would promote future breeding success (Telleria and Perez-Tris 2007). However, at smaller spatial scales such as the nest site, phainopeplas may select structural variables; the positive correlation between tree height and colonization probability may result from phainopeplas' preference for nesting and perching, and higher nest success, in tall trees (Krueger 1998, Crampton 2004). Regardless, due to low phainopepla density and likely scarce food, some patches with tall trees were unsuitable for breeding, thus abandoned. Phainopeplas may face a tradeoff at the landscape scale: acacias are shorter than mesquites, but support more berries. They may resolve this dilemma at smaller spatial scales, for example, by selecting taller trees within acacia patches (Crampton 2004).

Acacia and mesquite woodlands exhibited some spatial aggregation in our study area. Yet neither woodland type nor isolation was a strong predictor of woodland occupancy, suggesting that this aggregation was not a major factor behind the occupancy patterns we observed. All predictor variables (patch area, vegetation structure and food abundance) and response variables (phainopepla occupancy and density) varied greatly within the 'regions' of apparently aggregated woodlands.

Despite annual variation in total density and food abundance over the study area, distribution and density patterns within sites remained generally constant. This could result from two processes. Repeated extinctions and colonizations of some sites suggest that individuals could be site faithful to the extent that they reoccupy patches even if they become less suitable, as do painted buntings *Passerina ciris* (Lanyon and Thompson 1986). Alternatively, consistently occupied sites may be superior, and thus should be the focus of conservation attention (Sergio and Newton 2003). Apparently, phainopeplas, like other frugivores, are not naively site-faithful, but respond to spatial and temporal variation in habitat quality (Rey 1995, Oliver et al. 2003): 1) only 38% of banded phainopeplas returned over two years, often occupying a new territory (Crampton unpubl.); 2) some sites were occupied in one year only; and 3) during the 2002 drought, phainopeplas abandoned southern sites in their range, where mistletoe was less abundant (S. Spurrier pers. comm.). These observations suggest that most sites in our study area remained of relatively high

quality despite drought and reduced berry density in 2002. Ephemeral, apparently lower quality, sites were occupied by single, perhaps socially inferior, males (Marra 2000). Because similar factors, especially food abundance, determined occupancy and density, phainopepla conservation in this region should target consistently occupied, large, low elevation mesquite and acacia woodlands with abundant mistletoe berries. However, ephemeral patches may be critical to maintaining regional carrying capacity; for example, woodlands used in non-breeding seasons only may allow animals to be distributed more widely across available food resources until breeding begins.

Constrained by the tractability of assessing numerous ecological attributes simultaneously, few previous investigations have evaluated relative influences of two or more factors on animal distribution and abundance, or assessed how their roles might change over time. Food abundance should receive more attention in studies of animal distribution, which often focus on habitat structure and fragmentation, both of secondary significance in this study. Our results indicate that ecologists and conservation biologists should view habitat patches in terms of food distribution and abundance, not just structure and extent of the dominant vegetation community.

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Appendix 1. Study sites for phainopepla surveys in the northeastern Mojave Desert 2001–2003.

Site	General location	Zone	Easting ^A	Northing	Habitat	Patch area (ha)	Survey effort*			Nesting observed ^B
							2001	2002	2003	
AMG1	Amargosa Flat	11S	571405	4034679	Mesquite	32.2	N	Y	Y	
ARR1	Arrow Canyon	11S	688603	4073719	Acacia	516.0	Y	N	N	
ARR2	Arrow Canyon	11S	689155	4072239	Acacia	516.0	Y	Y	Y	
ARR3	Arrow Canyon	11S	689859	4071499	Acacia	516.0	Y	Y	Y	
ARR4	Arrow Canyon	11S	692028	4070438	Acacia	516.0	Y	N	N	
ASH2	Ash Meadows	11S	565205	4028773	Mesquite	2.5	N	Y	Y	
AVI1	near Ft Mojave	11S	714121	3880183	Mesquite	14.7	N	Y	Y	2002
AVI2	near Ft Mojave	11S	714961	3882790	Mesquite	6.6	N	Y	Y	probable
AZ91	along Arizona SR 91	12S	234557	4081742	Acacia	31.3	Y	Y	Y	2003
BBHQ	Big Bend of the Colorado S. P.	11S	714837	3888738	Mesquite	108.0	Y	Y	Y	
BBS	Big Bend of the Colorado S. P.	11S	715623	3885566	Mesquite	20.0	Y	Y	Y	2002-03
BLAC	near Roger Springs	11S	730027	4029408	Acacia	2.8	Y	Y	Y	suspected
BLU	near Blue Point Spring corner of Buffalo and	11S	730600	4030389	Mesquite	0.5	Y	N	N	
BUF	Washington	11S	656367	4005347	Acacia	1.4	N	Y (2x)	Y	
CAC	Cactus Springs	11S	614347	4048672	Mesquite	34.0	Y	Y	Y	
CAT	Catclaw Wash	11S	742589	4014942	Acacia	1.3	N	Y (2x)	Y (2x)	
CCR1	Corn Creek	11S	646309	4034507	Mesquite	355.0	Y	Y	Y	
CCR2	Corn Creek	11S	646591	4035669	Mesquite	355.0	Y	Y	Y	
CCR3	Corn Creek	11S	645573	4035609	Mesquite	355.0	Y	N	N	
CCR4	Corn Creek	11S	646826	4033921	Mesquite	355.0	Y	Y	Y	
CR1	China Ranch	11S	572309	3961465	Mesquite	15.0	N	Y	Y	
CSN1	near Coyote Springs	11S	678419	4095988	Acacia	900.0	Y	Y	Y	
CSN2	near Coyote Springs	11S	678362	4095486	Acacia	900.0	Y	Y	Y	
CSN3	near Coyote Springs	11S	678427	4092176	Acacia	900.0	Y	Y	Y	2001-03
CSN4	near Coyote Springs	11S	677986	4093432	Acacia	900.0	Y	Y	Y	2001-02
CWC1	near Cottonwood Cove	11S	695245	3927672	Acacia	17.0	Y	Y	Y	2003
DEV	Devil's Throat	11S	753051	4039242	Acacia	0.5	N	Y (2x)	N	
DRY	Dry Lake off I-15 N	11S	689541	4035356	Mesquite	6.7	Y	Y	N	
ELD4	El Dorado Wash	11S	682767	3951259	Acacia	100.0	Y	Y	Y	
EMP	Empire Wash	11S	706858	3910982	Acacia	75.0	Y	N	N	
FC	Valley of Fire S.P.	11S	726556	4034395	Acacia	1.7	Y	Y	Y	suspected
FL	Floyd Lamb S. P.	11S	655945	4021444	Mesquite	1.7	N	Y	Y	
FRA1	near Longstreet Casino	11S	551332	4027299	Mesquite	182.0	Y	Y	Y	
FRA2	near Longstreet Casino	11S	550614	4027992	Mesquite	182.0	Y	N	N	
FRA3	near Longstreet Casino	11S	548353	4030688	Mesquite	182.0	Y	N	N	
FRA4	near Longstreet Casino	11S	546624	4032512	Mesquite	182.0	Y	Y	Y	
GBW	Gold Butte Wash	11S	747708	4029130	Acacia	0.6	N	Y (1x)	N	
GRP	Grapevine Canyon	11S	709993	3900711	Acacia	1.5	Y	Y	Y	2001-03
HIK1	Hiko Wash	11S	705002	3894231	Acacia	83.4	Y	N	N	
HIK2	Hiko Wash	11S	707432	3894360	Acacia	83.4	Y	Y	Y	2003
HIK3	Hiko Springs	11S	710653	3894084	Acacia	35.0	Y	Y	Y	suspected
HIL1	Highland Mtns	11S	674284	3947794	Acacia	0.5	N	Y	N	
HIL2	Highland Mtns	11S	678853	3950617	Acacia	0.9	Y	Y	Y	
HIL3	Highland Mtns	11S	676656	3951571	Acacia	3.0	N	Y	Y	2002-03
KEL1	Kellog Rd, Pahrump	11S	599105	3997179	Mesquite	1.2	Y	Y	Y	
KEL2	Kellog Rd, Pahrump Las Vegas Springs	11S	599843	3996157	Mesquite	39.2	Y	Y	Y	2001-03
LVS1	Preserve	11S	662738	4004863	Mesquite	12.4	Y	Y	Y	2001-03
LWV1	Las Vegas Wash	11S	677256	3999427	Mesquite	1.0	N	Y	Y	
MEA1	Meadow Valley Wash	11S	716534	4063295	Mesquite	17.1	Y	Y	Y	near
MEA2	Meadow Valley Wash	11S	716118	4063933	Mesquite	17.1	Y	N	N	
MES1	Mesquite Lake	11S	624605	3953008	Mesquite	2500.0	N	Y	Y	
MES29	Mesquite Lake	11S	630961	3954686	Mesquite	2500.0	N	Y	Y	
MES3	Mesquite Lake	11S	625539	3956738	Mesquite	2500.0	N	Y	N	
MES39	Mesquite Lake	11S	632240	3952187	Mesquite	2500.0	N	Y	N	
MES4	Mesquite Lake	11S	629045	3950108	Mesquite	2500.0	N	Y	N	
MES8	Mesquite Lake	11S	623642	3953087	Mesquite	2500.0	N	Y	Y	2003
MTE1	near Moapa Tribal Store	11S	702612	4038162	Acacia	3.0	Y	N	N	
MTE2	near Moapa Tribal Store	11S	707037	4036038	Acacia	1.9	Y	Y	Y (2x)	

(Continued)

Appendix 1. (Continued)

Site	General location	Zone	Easting ^A	Northing	Habitat	Patch area (ha)	Survey effort*			Nesting observed [§]
							2001	2002	2003	
MUD2	Muddy River	11S	714960	4059740	Mesquite	30.2	Y	Y	Y	
MUD3	Muddy River	11S	714352	4059515	Mesquite	7.4	Y	Y	Y	
NEL2	Nelson	11S	696343	3954747	Acacia	3.7	Y	Y	Y	
NLV1	North Las Vegas	11S	663141	4018674	Acacia	3.1	Y	N	N	
NLV2	North Las Vegas	11S	664193	4018007	Acacia	3.5	Y	N	N	2001
NLV3	North Las Vegas	11S	663543	4017478	Acacia	2.6	Y	N	N	
NLV4	North Las Vegas	11S	665447	4017975	Acacia	9.5	Y	Y	Y	2001, 2003
OVT1	Overton	11S	730627	4044315	Mesquite	1.0	Y	Y	Y	2002-03
PA1	Pahrump	11S	587724	3997223	Mesquite	28.0	N	Y	Y	
PA3	Pahrump	11S	590804	3997531	Mesquite	5.6	N	Y	Y	
PA4	Pahrump	11S	592201	3996991	Mesquite	1.8	N	Y	Y (1x)	
PA5	Pahrump	11S	589228	4002169	Mesquite	13.4	Y	Y	Y	suspected
PA6	Pahrump	11S	581879	4011840	Mesquite	5.8	N	Y	Y	
PIU1	Piute Wash	11S	698605	3878484	Acacia	1400.0	Y	N	N	
PIU2	Piute Wash	11S	697726	3880829	Acacia	1400.0	Y	Y	Y	2001-03
PIU3	Piute Wash	11S	690331	3913991	Acacia	1400.0	N	Y	Y	
PIU4	Piute Wash	11S	690564	3912040	Acacia	1400.0	Y	Y	Y	2001-03
PIU5	Piute Wash	11S	693236	3907182	Acacia	1400.0	Y	Y	Y	2002
PSP	Piute Springs, MNP	11S	683836	3887614	Acacia	2.4	N	Y (1x)	N	
RAN2	Warm Springs Ranch	11S	704936	4065457	Mesquite	691.0	Y	Y	Y	2001-03
RAN3	Warm Springs Ranch	11S	705833	4066056	Mesquite	691.0	Y	Y	Y	suspected
RAN4	Warm Springs Ranch	11S	704468	4066642	Mesquite	691.0	Y	Y	Y	2001-03
RES	Resting Springs	11S	574628	3969108	Mesquite	15.0	N	Y (3x)	Y	
ROG	Roger Springs	11S	729316	4028866	Mesquite	2.8	Y	Y	Y	
ROM	Roman Wash	11S	705515	3909697	Acacia	16.8	Y	Y	Y	2001-03
RSP	Red Springs	11S	642076	4001216	Acacia	0.7	N	Y	Y	2002-03
SAC	Sacaton Wash	11S	711544	3902354	Acacia	45.2	Y	Y	Y	2001-02
SAN1	Sandy	11S	618828	3969104	Mesquite	65.5	Y	Y	Y	
SAN2	Sandy	11S	618657	3969768	Mesquite	65.5	Y	N	N	
SLS	Slaughterhouse Springs, MNP	11S	656901	3909343	Mesquite	0.6	N	Y (1x)	N	
STE	Stewart Valley	11S	574436	4012765	Mesquite	110.0	Y	Y	Y	
STP1	Stump Springs	11S	606398	3983943	Mesquite	355.0	Y	Y	Y	
STP2	Stump Springs	11S	605497	3983198	Mesquite	355.0	Y	Y	Y	
STP3	Stump Springs	11S	606963	3984917	Mesquite	355.0	Y	N	N	
STP4	Stump Springs	11S	607847	3981878	Mesquite	355.0	Y	Y	N	
SUN1	Sunset Park	11S	670172	3992921	Mesquite	18.4	Y	Y	Y	2002-03
TCH1	Techaticup Wash	11S	701044	3954013	Acacia	0.6	Y	Y	Y	2003
TCH2	Techaticup Wash	11S	697705	3955285	Acacia	50.3	Y	N	N	2001
TOQ1	Toquop Wash	11S	751514	4070908	Acacia	16.4	Y	Y	Y	
VOF	Valley of Fire S.P.	11S	720327	4033227	Acacia	6.7	Y	N	N	
VR1	Virgin River near Riverside	11S	742368	4062247	Mesquite	0.5	N	Y	Y	
VR2	Virgin River near Riverside	11S	747781	4067954	Acacia	0.5	N	Y	Y	
WG	Valley of Fire S.P.	11S	718602	4031711	Acacia	5.6	Y	Y	Y	2001-02
WWS1	west of Warm Springs	11S	697727	4071044	Acacia	10.8	Y	Y	Y	
WWS2	west of Warm Springs	11S	701248	4069241	Acacia	72.9	Y	N	N	

^A Eastings and Northings are in NAD 83

* in FS 1, survey effort varied between 1-4 visits. In FS 2 and 3, sites were generally visited at least 4 times, and we have noted any visited less often.

§ probable=many pairs present throughout breeding season; suspected=saw young with parents