

NEST-HABITAT SELECTION BY THE PHAINOPEPLA: CONGRUENCE ACROSS SPATIAL SCALES BUT NOT HABITAT TYPES

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Abstract. Animals select habitat to satisfy life-history requirements, yet few habitat-selection studies consider multiple factors, especially food. Because resources vary in abundance and quality across different spatial scales or habitat types, selected habitat features may also vary, making habitat selection incongruent. Using an information-theoretical approach, we assessed whether Phainopeplas (*Phainopepla nitens*) select breeding habitat for food abundance or vegetation structure at nest-tree and nest-patch scales in two woodland types, acacia and mesquite, in the Mojave Desert. Habitat selection at the tree and patch scales was congruent: models containing both food (mistletoe) and structure variables had stronger support than models with only food or structure variables. In both woodland types, nest trees were larger and had more food, and in nest patches food abundance, tree density, tree height, and cover were greater than in non-nest patches. However, nests in acacia were higher than those in mesquite, acacia nest trees were smaller and had more food but less cover, and acacia nest patches had lower tree density and more food. These differences between woodland types apparently led to incongruence in nest-site selection: the difference between height of nest and non-nest trees was greater in shorter acacia than in mesquite woodlands, and the difference in food abundance between nest and non-nest sites was greater in food-poor mesquite woodlands. Contrary to assertions that vegetation structure drives nest-site selection, Phainopeplas' nest-site selection reflects both food abundance and vegetation structure at all spatial scales, underscoring the importance of multiple factors, scales, and habitats to habitat-selection studies.

Key words: nest site, mesquite, mistletoe, food availability, habitat structure, hierarchical habitat selection, acacia, *Phainopepla nitens*.

Selección del Hábitat de Anidación por *Phainopepla nitens*: Congruencia a través de Escalas Espaciales pero no de Tipos de Hábitat

Resumen. Los animales seleccionan el hábitat para satisfacer los requerimientos de sus historias de vida, pero pocos estudios de selección de hábitat consideran múltiples factores, especialmente relacionados al alimento. Debido a que los recursos varían en abundancia y calidad a través de diferentes escalas espaciales o tipos de hábitat, los rasgos seleccionados del hábitat también pueden variar, haciendo que la selección del hábitat sea incongruente. Usando un enfoque basado en la teoría de la información, evaluamos si *Phainopepla nitens* selecciona los hábitats de anidación por la abundancia de alimentos o por la estructura de la vegetación a las escalas del árbol donde se ubica el nido y del parche donde se ubica el nido en dos tipos de bosque, acacia y mesquite, en el desierto de Mojave. La selección de hábitat a las escalas de árbol y de parche fue congruente: los modelos que contenían tanto variables de alimento (muérdago) como estructurales tuvieron un mayor apoyo que los modelos con sólo variables de alimento o variables estructurales. En ambos tipos de bosque, los árboles con nidos fueron mayores y tuvieron una mayor cantidad de alimento, y en los parches con nidos la abundancia de alimentos, la densidad de árboles, la altura de los árboles y la cobertura fueron mayores que en los árboles y parches sin nidos. Sin embargo, los nidos en acacia estuvieron más altos que en mesquite, los árboles de acacia con nidos fueron más pequeños y tuvieron mayor cantidad de alimento pero menos cobertura, y los parches de acacia con nidos tuvieron menor densidad de árboles y mayor cantidad de alimento. Estas diferencias entre los tipos de bosque llevan aparentemente a una incongruencia en la selección de los sitios para los nidos: la diferencia entre la altura de los árboles con nido y sin nido fue mayor en los bosques de acacia, que son de menor altura que los bosques de mesquite, y la diferencia en la abundancia de alimento entre sitios con y sin nidos fue mayor en los bosques de mesquite, que son más pobres en alimento. Contrariamente a las aseveraciones de que la estructura de la vegetación condiciona la selección de los sitios de anidación, la selección de los sitios de anidación por *P. nitens* refleja tanto la abundancia de alimento como la estructura de la vegetación a todas las escalas espaciales, poniendo de manifiesto la importancia de considerar múltiples factores, escalas y ambientes en los estudios de selección de hábitat.

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INTRODUCTION

Selection of habitat is a complex multivariate process based on several factors and cues at multiple scales (Johnson 1980, Kristan et al. 2007), including the availability of food, water, mates, nest sites, or shelter. Because such resources may not be available in the same patch or occur at the same spatial scale, habitat selection may represent a tradeoff between, or a maximization of, the abundance of different resources. Selected habitat may contain a mixture of patches of different sizes, with the animal commuting between patches (Orians and Wittenberger 1991, Bissonette et al. 1997). In other words, because most organisms experience and respond to a hierarchy of environmental patchiness (Kotliar and Wiens 1990), habitat selection also is hierarchical, at the largest scale involving choice of a general place to live (geographical range), and at successively finer scales including selection of home range and habitat patches (Johnson 1980, Orians and Wittenberger 1991). Congruent hierarchical habitat selection maintains selection of habitat features across scales (e.g., Schaefer and Messier 1995, Myrsterud et al. 1999, Jenkins et al. 2007), whereas in incongruent habitat selection, certain habitat features may be selected at one scale but not another (McLoughlin et al. 2002, 2004, Morin et al. 2005, Barg et al. 2006). Assessing congruence is an important ecological question, as there is debate about whether coarse-scale or fine-scale habitat features are more critical to fitness (Orians and Wittenberger 1991, Rettie and Messier 2000); from a management perspective, this assessment is essential for ensuring that all necessary habitat elements are targeted at appropriate scales.

The idea of hierarchical habitat selection dates back at least to Hilden (1965), but it did not receive much empirical attention until recently (e.g., Orians and Wittenberger 1991, Bissonette et al. 1997, Morin et al. 2005, Bailey and Thompson 2007). Multifactor studies, for example, those evaluating the roles of both food and shelter, are even less common than empirical studies of hierarchical habitat selection. In particular, the importance of food abundance relative to other factors in habitat selection was neglected until recently (but see Jansen et al. 2001, Kwit et al. 2004, Doran and Holmes 2005, Cameron and Cunningham 2006, Rodewald and Brittingham 2007, Smith et al. 2007).

Although large-scale habitat choices may constrain options available at finer scales (Hutto 1985), within those finer scales habitat selection may be dominated by the resource with the most limited distribution—usually the nest or breeding site (Orians and Wittenberger 1991, but see Rettie and Messier 2000). Because nest predation is the primary cause of nest failure for most birds (Ricklefs 1969), it has been posited that birds select nest sites primarily for vegetation structure that mitigates the nest's susceptibility to predation (Martin and Roper 1988, Martin 1993), a hypothesis supported by some studies (Martin and Roper 1988, Liebezeit and George 2002) but not others (Holway 1991, Siepielski et al. 2001). These

differences may arise from a failure to consider relevant spatial scales, such as landscape-level variation in habitat structure or the suite of predators, or other processes that may shape habitat selection (Sakai and Noon 1991, Siepielski et al. 2001). Nest microclimate, also influenced by vegetation structure, affects parental energy expenditure (Walsberg 1981) and development and survival of chicks (Austin 1974). Food availability, which affects clutch size, nestling growth, and other aspects of fecundity (Martin 1987, Simons and Martin 1990, Howe et al. 1996), also may affect habitat selection (Lenington 1980, Sedgwick and Knopf 1992). Consideration of only fine scales or vegetation structure is likely to lead to an incomplete, even misleading, picture of habitat selection (Kotliar and Wiens 1990, Orians and Wittenberger 1991).

We investigated the interplay between food abundance and vegetation structure (presumed to affect nest microclimate and predation risk) to determine if nest-site selection by the Phainopepla (*Phainopepla nitens*) was congruent across spatial scales (nest tree and patch) and between two types of woodland. We chose the Phainopepla as a model system for several reasons. First, in our study area, Phainopeplas inhabit only two simple but distinct woodland types: those dominated by mesquite (*Prosopis glandulosa* and *P. pubescens*) and those dominated by acacia (*Acacia greggii*). Both types contain few, if any, other arborescent species and are restricted to the desert's scarce riparian areas. Thus they represent islands of habitat in the matrix of desert scrub that are much more easily defined than many woodland types in other landscapes. Second, both acacia and mesquite are infected by desert mistletoe (*Phoradendron californicum*). Desert mistletoe berries, which vary in abundance within and among patches, constitute the predominant food of Phainopeplas breeding in the desert, although the birds consume some insects (Chu and Walsberg 1999). Berry abundance is the primary predictor of the Phainopepla's habitat selection at the landscape scale and also strongly influences many aspects of its reproductive success, whereas insect abundance influences only nest initiation (Walsberg 1977, Chu and Walsberg 1999, Crampton 2004). Thus Phainopeplas may select nest sites with abundant mistletoe. Yet Phainopeplas build open cup nests, a nest type often subject to predation (Martin and Li 1992), and during the breeding season they are faced with extreme temperatures, suggesting that they may select sites with vegetation structure that mitigates these two factors.

Our overall objective was to assess evidence for congruence in selected characteristics of nest sites at the scales of the nest, tree, and patch and between the two woodland types. We use "nest site" to encompass all spatial scales. First, we compared nest sites in mesquite and acacia woodlands, hypothesizing that they differ in both food abundance and vegetation structure since the woodlands themselves differ in those attributes (Crampton 2004). Second, we determined if and how nest sites selected by Phainopeplas at various scales differed from non-nest sites. We hypothesized that food (mistletoe)

abundance and vegetation structure influence habitat selection at different scales, resulting in incongruent habitat selection. We predicted that only vegetation structure (not food abundance) would differentiate nest trees from non-nest trees, because at this scale structure might influence nest predation and microclimate, while foraging at the nest might attract predators and is not correlated with nest survival (Martin 1993, Martin et al. 2000, Crampton 2004). However, we predicted that both structure and food abundance would be important at the larger spatial scale of the 0.04-ha patch around the nest tree, in which parents would be able to forage near the nest without attracting too much attention to it. We also hypothesized that if food abundance or vegetation structure of the woodland types differs, their relative importance would vary, i.e., *Phainopepla*s would compensate for these differences in their choice of nest sites. For example, we predicted that if food were less abundant in mesquite, it would influence habitat selection more heavily in mesquite than in acacia woodlands, leading to a lack of congruence in habitat selection across woodland types.

Identifying factors that determine the *Phainopepla*'s nest-site selection is not only an interesting ecological question but an important conservation issue. In Nevada and Arizona, the *Phainopepla* appears to be declining because of habitat loss (Sauer et al. 2005). In Nevada, it is considered a sensitive species by the Bureau of Land Management (BLM 1998), and a covered species in the Clark County Multiple Species Habitat Conservation Plan (Recon 2000). This study will help identify features of these desert woodlands that provide high-quality nesting habitat and thus inform the species' conservation and management.

METHODS

STUDY AREA AND STUDY SITES

The study area comprised several mesquite and acacia woodlands in the northeastern Mojave Desert (Clark Co. in southern Nevada near Las Vegas and San Bernardino Co. in southeastern California, an area of ~21 000 km²), where *Phainopeplas* breed between early February and early June (Fig. 1). These woodlands exist in a matrix of desert scrub, in areas of high groundwater or runoff. Annual precipitation averages 10–15 cm,

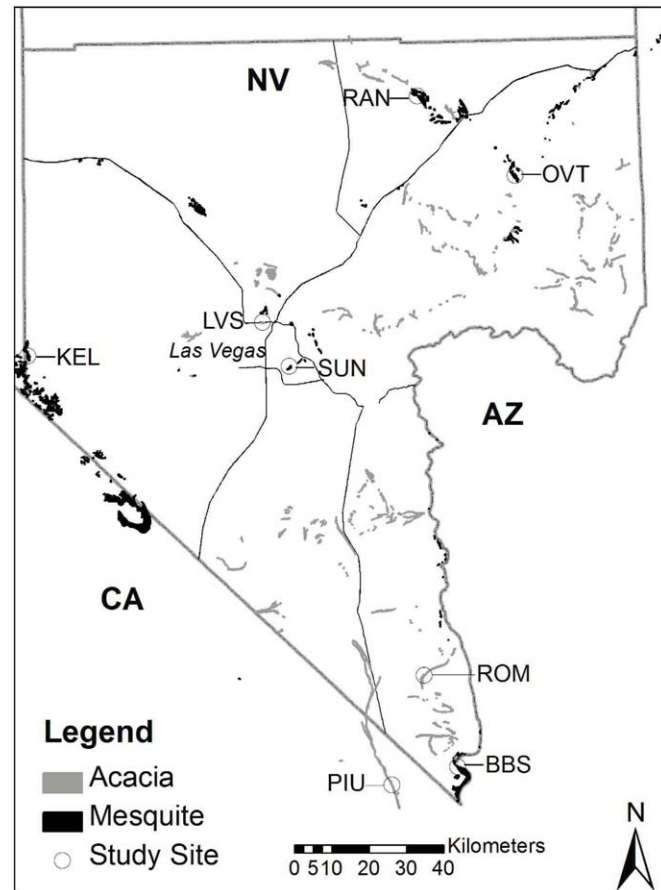


FIGURE 1. Mesquite and acacia woodlands in the study area. Circles, study sites used to assess the *Phainopepla*'s nest-site selection.

and temperatures range from -5°C to 48°C (Krueger 1998). From 76 woodlands used in a companion study to this study (Crampton et al. 2011), we used a stratified random approach to select eight woodlands (four in 2001, four in 2002) so that they (1) sustained at least four breeding pairs each, (2) were distributed throughout the study area, (3) consisted of both acacia and mesquite woodland, and (4) represented a variety of patch sizes (from 12 to 1000 ha; Table 1, Fig. 1). Although woodlands were dominated by either honey mesquite or catclaw acacia (called

TABLE 1. Characteristics of study sites in the northeastern Mojave Desert at which we monitored *Phainopepla* nests and measured habitat characteristics in 2001, 2002, and 2003. All UTM coordinates are in zone 11N, NAD83.

Site	Easting	Northing	Elevation (m)	Woodland type	Species of non-host trees and nest plants present	Woodland size/plot size (ha)	No. nest/non-nest trees
LVS	662738	4004863	635	mesquite	<i>Populus, Salix, Fraxinus</i>	12/10	15/7
SUN	670172	3992921	612	mesquite	<i>Populus</i>	16/15	18/7
OVT	730627	4044315	384	mesquite	<i>Tamarix, Populus</i>	20/14	12/8
BBS	715623	3885566	166	mesquite	<i>Tamarix, Fraxinus</i>	20/14	17/7
KEL	599843	3996157	888	mesquite	none	250/15	29/9
RAN	704936	4065457	542	mesquite	<i>Populus, Salix, Tamarix</i>	700/12	14/9
ROM	705515	3909697	834	acacia	<i>Chilopsis, Juniperus, Yucca</i>	200/15	20/12
PIU	697726	3880829	570	acacia	<i>Opuntia</i>	1000/11	22/10

“host” trees because they can support desert mistletoe), small numbers of trees of other species occurred in some woodlands (Table 1). Within each woodland, we established a 10- to 15-ha study plot around a randomly located transect used to census *Phainopepla* density by Crampton et al. (2011); the exact size and shape of the study plot varied to ensure it was occupied by at least four pairs of *Phainopeplas* (Table 1).

NEST MONITORING

We located and monitored nests from 2001 to 2003 according to methods described in Martin and Geupel (1993). Beginning in February of each year, we attempted to locate all *Phainopepla* nests within each study plot, using a combination of random searches, behavioral cues of adults, and territory mapping. We mist-netted as many *Phainopeplas* as possible in each study plot and color-banded them with a unique combination to map territories and track the number and location of nests the birds attempted each year. Every 3–5 days, we viewed the nest from a distance to see if it was still active; while monitoring near the expected date of hatching or fledging, we briefly visited the nest to count the eggs or chicks. As only 20 pairs (12%) constructed more than one nest, we included in statistical analyses only the first active (≥ 1 egg laid) nest of each pair.

INSECT SAMPLING

To control for the possibility that differences in insect abundance might influence nest-site selection, in 2002 and 2003, we assessed whether insect abundance varied within and among plots and between years by hanging 3- \times 5-inch sticky traps at four random locations in each study plot. We hung these traps once a week for 4 days during the several-week period when nests contained nestlings (23 Mar–25 May 2002; 23 Feb–11 Jun 2003) and assumed that if insect abundance were consistent within plots at this time it would be consistent within plots at the time of nest selection. To estimate insect abundance, we assigned insects to three size classes: < 4 mm, 4–7.9 mm, and ≥ 8 mm; we observed *Phainopeplas* catching insects of all classes. Because insects < 4 mm long were very abundant, we subsampled them by dividing the trap into eight equal sections. We randomly selected four sections in which we counted all insects < 4 mm, then multiplied that number by 2. Then, we counted all insects in the second class and counted and recorded the length of all insects in the third. We estimated total insect abundance as $(\# \text{ insects } < 4 \text{ mm}) \times 2 \times 2 \text{ mm} + (\# \text{ insects } 4\text{--}7.9 \text{ mm}) \times 6 \text{ mm} + (\text{sum of lengths of insects } \geq 8 \text{ mm})$.

SAMPLING OF NEST TREES AND PATCHES

Upon discovering a nest, if disturbance was likely to be minimal, we quickly estimated berry abundance and mistletoe volume on the nest tree as described below. Between late April and early June, after nests had fledged or failed, we fully characterized the vegetation structure and berry resources of nest trees and patches and of non-nest trees and patches (see below). The timing of this characterization provided a fair

assessment of available nest sites at the time of selection, as (1) berry abundance on those trees measured both at nest discovery and completion did not change (paired *t*-test, $t_{68} = -1.46$, $P = 0.15$) and (2) cover at nest sites typically was constant throughout the breeding season, provided by mistletoe and branches, not by leaves (see Results). Many host trees (64% in 2002 and 55% in 2003) did not leaf out until after fledging/failure and after our measurements were taken. Moreover, leaves of host trees are small and do not provide much cover even when present. We did not record these data for inactive nests. We measured fewer habitat variables in 2001 (see below), so data from this year serve primarily descriptive purposes.

At the nest scale, in all years, we measured height of the nest from the ground. In 2002 and 2003, we measured distance of the nest from the trunk and to the edge of the canopy and the nest's compass orientation relative to the trunk. We noted if the nest was in a mistletoe and visually estimated what proportion of the nest was visible from above, below, and in each cardinal direction from a distance of 1 m. We averaged these estimates to generate a mean percentage concealment score.

At the scale of the nest tree, we noted species and measured tree height in all years. In 2002 and 2003, we measured the tree's maximum width, or crown diameter, and estimated percent cover in a 5-m radius of the nest. For the latter, we extended meter tapes at nest height from the nest to a distance of 5 m in each of the cardinal directions and noted if vegetation (mistletoe, branches, or leaves) vertically intersected the tapes at each 1-m horizontal interval for a total of 20 possible intercepts, which we converted into a percent cover score. Tree height, crown diameter, and this percent cover score represented vegetation structure at the tree scale. To estimate food abundance at this scale, we counted berries in tens up to 100 berries, then visually estimated the number of groups of 100 berries on each mistletoe plant. We then categorized berry abundance as 0, 1–9, 10–49, 50–99, 100–499, 500–999, and so on, up to $> 100\,000$ berries; in analyses, we used the maximum value of each category because we assumed that some berries had been eaten during the study period. We verified our estimates with those made independently by other trained observers; estimates were always in the same category.

At the nest-patch scale, in 2002 and 2003 we tallied all trees in a 11.3-m-radius circular plot ($= 0.04$ ha) around the nest that were infected by mistletoe in 1-m height categories (< 1 m, < 2 m, etc.) and noted if the mistletoe had berries. We tallied all uninfected trees in 2-m height categories. We used the total number of trees in each height category as a measure of vegetation structure and the number of trees with berries as a measure of food abundance. Also at this scale, we identified the mistletoe-infected tree nearest the nest tree in each of the four cardinal quadrants (“adjacent” trees), providing such a tree existed in a 30-m radius (the average territory size; Walsberg 1977). For each adjacent tree, we noted height and distance to nest tree as measures of vegetation structure and estimated number of berries to represent food abundance. We

calculated the mean height and distance, and summed berries, across all adjacent trees around each nest tree.

SAMPLING OF NON-NEST TREES AND PATCHES

To determine if Phainopeplas selected nest sites for certain characteristics (i.e., food, vegetation structure), in 2002 we randomly selected 8–12 (depending on the number of nests and the area of the plot) non-nest host trees in five of the study plots. In our plots, Phainopeplas usually (95% of nests) nested in host trees infected by mistletoe, so 95% of our sample of non-nest trees was composed of infected host trees and 5% was composed of uninfected host trees. In 2003, we re-estimated all mistletoe variables for these trees and sampled 8–12 new non-nest host trees in the remaining three study plots. To select non-nest trees, we generated 8–12 random GPS points in each plot and located the nearest infected plant to the point for

95% of the sample; thereafter, we selected the nearest uninfected tree.

Between late April and early June, we measured the suite of tree, patch, and adjacent-tree variables described above at each non-nest tree. For those measurements that in a nest tree were centered on a nest (e.g., 5-m % cover), in non-nest trees we randomly selected a distance and bearing from the trunk, halfway up the tree (the typical nest height; see Results below), from which to make measurements.

HYPOTHESES FOR STATISTICAL ANALYSES

At the nest scale, we evaluated two hypotheses (Table 2): (1) Nest sites are oriented at random with respect to the trunk of the nest tree; (2) nest sites are higher in comparison total tree height in acacia trees than in mesquite trees because acacias are shorter than mesquites.

TABLE 2. Description of hypotheses and predictions for Phainopepla nest-site selection and differences between nest sites in acacia and mesquite woodlands in the northeastern Mojave Desert, 2001–2003. See footnotes for additional details.

Hypothesis	Hypothesis details	Spatial scale	Test	Global model	Prediction	Results table
1	Nest orientation random with respect to trunk	nest	χ^2	—	—	—
2	Nest height in acacia and mesquite trees differs	nest	<i>t</i> -test	nest height = woodland	higher in mesquite	—
3	Nest sites differ by woodland type ^a	woodland	logistic regression	woodland = year + food + food × year + structure	structure + food in top model	Tables 4 and 5
4	Nest-site selection is incongruent between scales ^b	tree/patch	compare Tables 6 and 7	—	top models differ	Tables 6 and 7
4a	Nest trees selected on basis of structure ^c	tree	logistic regression	site type = year + woodland + food + food × year + food × woodland + structure + structure × woodland	structure in top model	Table 6
4b	Nest patches selected on basis of structure + food ^d	patch	logistic regression	site type = year + woodland + food + food × year + food × woodland + structure + structure × woodland	structure + food in top model	Table 7
5	Nest-site selection differs by woodland type ^e	tree/patch	logistic regression	Site type = year + woodland + food + food × year + food × woodland + structure + Structure × woodland	interactions in top model	Tables 6 and 7

^aGlobal model included food and structure variables as main effects, with year as a covariate. We predicted both food and structure variables (and possibly year) would be included in top models for both nest trees and patches.

^bWe tested this hypothesis by comparing model-selection results for site selection at the tree and patch scales. We predicted that the top models would differ as outlined in footnotes c and d (i.e., incongruent selection).

^cGlobal model included food and structure variables as main effects, with year and woodland type as covariates. We predicted that only structure variables (with or without covariates and interactions) would appear in top models.

^dGlobal model included food and structure variables as main effects, with year and woodland type as covariates. We predicted that all main effects (with or without covariates and interactions) would be included in top models.

^eGlobal model included main effects, covariates described above, and interactions between covariates and main effects. We predicted that top models would contain interaction terms, indicating differences between woodland types in selection for some (or all) attributes.

At the tree and patch scales and between mesquite and acacia, we used an information-theoretical approach to evaluate three complementary a priori hypotheses about the Phainopepla's nest-site selection (Table 2):

- (3) Nest sites differ by woodland type (i.e., are incongruent), because the woodlands themselves differ in food abundance and vegetation structure. We predicted that nest sites (trees and patches) in mesquite should have bigger trees with more cover but less food than those in acacia.
- (4) Nest sites differ from non-nest sites in scale-specific ways; i.e., nest selection at the tree and patch scales is incongruent. For reasons discussed in the Introduction, we expected that food and vegetation structure were important at different scales, so we developed two sub-hypotheses:
 - (4a) Nest *trees* differ from non-nest trees more in vegetation structure than in food abundance. Specifically, we predicted that nest trees should be taller and wider and have more cover than non-nest trees (to decrease both predation risk and thermal stress; see Martin 1993).
 - (4b) Nest *patches* differ from non-nest patches in both food resources and vegetation structure. We predicted that nest patches should have higher food abundance, taller trees, and more cover than non-nest patches.

- (5) Nest-site selection in the two woodland types is incongruent. We predicted that if woodlands differ in food abundance and vegetation structure, then Phainopeplas should compensate for these differences in nest-site selection at both tree and patch scales, as suggested in the Introduction. This hypothesis was modeled statistically by interaction terms between woodland type and food abundance or structure and was evaluated simultaneously with hypothesis 4.

STATISTICAL ANALYSES

At the nest scale, to test H1 (random orientation of nests), we categorized nests by subcardinal compass orientation and used a χ^2 analysis with $\alpha = 0.05$ in PROC FREQ (SAS 2001). To assess hypothesis 2 (nest height in acacia vs. mesquite), we used a *t*-test.

To test hypotheses 3–5, we ranked sets of multiple logistic-regression models containing different combinations of food and structure variables with Akaike's information criterion adjusted for small sample sizes (AIC_c , Burnham and Anderson 2002) in PROC LOGISTIC (SAS 2001). Structure variables included height, crown diameter, cover, and density. Food included variables representing berry abundance (Table 3). The best model had the smallest AIC_c , and we ranked all

TABLE 3. Least-square means (\pm SE) for variables measured at and around Phainopepla nest (N) and non-nest (U) trees at acacia and mesquite sites, 2002 and 2003. Food variables are italicized, while structure variables are in roman font; $n = 89$ nest and non-nest trees in acacia, 169 nest and non-nest trees in mesquite, 87 nest and non-nest patches in acacia, and 166 nest and non-nest patches in mesquite.

		Acacia	Mesquite
Variable	Tree type	Mean \pm SE	Mean \pm SE
Tree scale			
Tree height (m)	N	2.71 \pm 0.10	4.45 \pm 0.12
	U	1.90 \pm 0.06	3.85 \pm 0.14
Crown diameter (m)	N	6.41 \pm 0.35	9.53 \pm 0.39
	U	4.69 \pm 0.73	9.52 \pm 0.68
5 m % cover	N	44.0 \pm 2.4	77.0 \pm 1.8
	U	26.1 \pm 1.7	60.8 \pm 2.9
<i>Total berries</i>	N	5755 \pm 1172	1593 \pm 443
	U	1027 \pm 396	200 \pm 66
Patch scale			
Mean height of adjacent trees (m) ^a	N	2.47 \pm 0.29	3.96 \pm 0.13
	U	2.18 \pm 0.07	3.93 \pm 0.11
Mean distance to adjacent trees (m)	N	9.12 \pm 0.62	9.95 \pm 0.50
	U	10.1 \pm 0.87	11.7 \pm 0.79
<i>Total number of berries on adjacent trees</i>	N	9008 \pm 1087	2892 \pm 778
	U	5316 \pm 1026	661 \pm 240
<i>Number of trees with berries within patch</i>	N	4.4 \pm 0.5	3.0 \pm 0.3
	U	3.3 \pm 0.5	0.9 \pm 0.3
Number of trees 1–3 m tall within patch ^a	N	5.6 \pm 0.6	1.7 \pm 0.3
	U	5.3 \pm 0.7	1.0 \pm 0.1
Number of trees 3–5 m tall within patch	N	2.7 \pm 0.3	3.8 \pm 0.5
	U	0.3 \pm 0.2	1.8 \pm 0.2
Percent cover within patch	N	28.4 \pm 1.3	58.1 \pm 2.3
	U	28.8 \pm 1.8	46.6 \pm 2.5

^aVariables used to rank woodland types (not nest vs. non-nest sites) only.

TABLE 4. Summary of rankings of all candidate models from multiple logistic regression assessing differences in Phainopepla nest sites by woodland type (acacia vs. mesquite) at the tree scale in 2002 and 2003 (hypothesis 3). "Structure" models include the variables tree height (m), tree-crown diameter (m), and percent cover within 5 m; "food" models include the variables berry abundance, plus berry abundance \times year if indicated. "All" models include all structure and food variables, plus food \times year if indicated. Models representing our predictions for this scale are italicized. The response variable was mesquite = 0, acacia = 1. Sample size, n = 104 mesquite and 43 acacia trees, K = number of parameters, w_i = Akaike weight.

Model	K	ΔAIC_c^a	w_i
<i>All (structure + food + year + interaction)^b</i>	7	0.00	0.61
<i>All but year and year \times food</i>	5	1.82	0.25
<i>All, no interaction</i>	6	2.89	0.14
Structure + year	5	14.70	0.00
Food + year, no interaction	3	88.46	0.00
Food + year + interaction	4	88.68	0.00
Year (base)	2	104.98	0.00

^aLowest AIC_c = 75.3

^bSee Table 5 for terms, coefficients, and standard errors of coefficients for this top model.

other models by the difference between the values of their AIC_c and that of the best model (ΔAIC_c). The smaller the ΔAIC_c of subsequent models with respect to the top model, the more support they had: substantial support for models with ΔAIC_c = 0–2 and moderate support for models with ΔAIC_c = 4–7 (Burnham and Anderson 2002). We also used Akaike weights (w_i) to evaluate the relative importance of models (Burnham and Anderson 2002). This approach allowed us to select the most parsimonious model(s) describing nest-site selection. All global models satisfied the Hosmer–Lemeshow (2003) goodness-of-fit test and tests for overdispersion provided in SAS (2001). We present regression coefficients (\pm SE) of the top logistic-regression model in the text and in Table 5. Positive coefficients indicated that variables were positively correlated with mesquite (not acacia) or non-nest (not nest) sites. The direction and magnitude of coefficients for covariates in the top model(s) allowed us to assess the evidence for our predictions for the hypotheses 3, 4a, 4b, and 5.

To determine if nest sites differed by woodland type (hypothesis 3), at the tree and patch scales we constructed and ranked (a) base model (year only), (b) base + structure variables only, (c) base + food variables only, (d) all variables: base + food + structure, and (e) all variables but base (this model assessed annual variation in nest-site selection). We ranked seven tree-scale models (because we included food \times year interactions) and five patch-scale models, with the all-variable models representing our prediction for this hypothesis (Tables 4, 5, 6). The global or all-variable model for the tree scale was woodland type = structure + food + year + food \times year, where tree structure included tree height (m), crown diameter (m),

TABLE 5. Coefficients and standard errors of terms in top models.

Model	Variable	Coefficient	SE
Woodland type, tree scale: all (structure + food + year + interaction)			
		2.02	0.49
	year 2002	–0.54	0.37
	berry	–1.10	0.33
	berry \times 2002	0.64	0.30
	height	1.90	0.64
	crown	0.97	0.84
	cover	2.77	0.62
Woodland type, patch scale: all but year			
		10.8	5.54
	berry (on adjacent trees)	–6.56	3.67
	berry (in nest patch)	1.16	3.95
	mean height (of adjacent trees)	2.07	1.30
	mean distance (to adjacent trees)	2.94	1.74
	number of trees 1–3 m tall	–31.1	17.5
	number of trees 3–5 m tall	15.8	9.34
	cover	14.2	7.22
	number of infected trees	6.27	3.63
Nest vs. non-nest, tree scale: all (structure + food + base + all interactions)			
		3.91	0.83
	year 2002	–0.99	0.43
	acacia	–2.27	0.76
	berry	–3.74	1.29
	berry \times 2002	–2.29	1.23
	berry \times acacia	1.40	0.68
	height	–1.89	0.69
	crown	0.03	0.25
	cover	–1.98	0.52
	height \times acacia	–1.40	0.69
	crown \times acacia	–0.54	0.25
	cover \times acacia	0.83	0.52
Nest vs. non-nest, patch scale: all (structure + food + base + woodland interactions with structure)			
		1.44	0.77
	year 2002	–0.37	0.17
	acacia	–0.39	0.78
	berry (on adjacent trees)	–1.12	0.31
	berry (in nest patch)	–1.49	0.35
	mean distance (to adjacent trees)	–0.42	0.20
	number of trees 3–5 m tall	–4.55	0.98
	cover	0.052	0.55
	number of trees 3–5 m tall \times acacia	–3.93	0.99
	cover \times acacia	0.65	0.55

and percent cover within 5 m. For the patch scale, the global model was woodland type = structure + food + year, where patch structure was represented by mean height of adjacent trees (m), mean distance to adjacent trees (m), number of trees 1–3 m high, number of trees 3–5 m high, and percent cover at the patch scale. Woodland type was a categorical response variable with values mesquite = 0, acacia = 1.

TABLE 6. Summary of rankings of all candidate models from multiple logistic regression assessing differences in *Phainopepla* nest patches by woodland type (acacia vs. mesquite) at the patch scale in 2002 and 2003 (hypothesis 3). “Structure” models include the variables mean height of adjacent trees (m), mean distance to adjacent trees (m), number of trees 1–3 m high, number of trees 3–5 m high, and percent cover at the patch scale. “Food” models include the variables berry abundance of adjacent trees and number of trees with berries at the patch scale. “All” models include all structure and food variables, plus year if indicated. Models representing our predictions for this scale are italicized. The response variable was mesquite = 0, acacia = 1. Sample size, n = 96 mesquite and 41 acacia nest patches, K = number of parameters, w_i = Akaike weight.

Model	K	ΔAIC_c^a	w_i
<i>All but year^b</i>	8	0.00	0.74
<i>All (structure + food + year)</i>	9	2.09	0.26
Structure + year	7	16.04	0.00
Berry + year	4	114.78	0.00
Year (base)	2	135.16	0.00

^aLowest AIC_c = 35.

^bSee Table 5 for terms, coefficients, and standard errors of coefficients for this top model.

To assess congruence in nest-site selection across spatial scales (hypothesis 4) and between woodland types (hypothesis 5), at the tree and patch scales we constructed and ranked (a) base model (year + woodland type), (b) base + structure variables only, with and without interactions, (c) base + food variables only, with and without interactions, (d) all variables: base + food + structure, with and without interactions, and (e) all but base variables (Tables 5, 7, 8). The various two-way interactions of food and structure variables with woodland type evaluated congruence between woodland types (hypothesis 5) in that they indicated whether selected attributes differed by woodland type (i.e., whether nest sites differed from non-nest sites more in one woodland type than in the other). Site type (nest = 0, non-nest = 1) was the response variable. At the tree scale, we ranked nine models, with the base + structure and base + structure + interactions models corresponding to our prediction for hypothesis 4a (i.e., nest trees differ from non-nest trees in vegetation structure); the latter also specifically tested the prediction for hypothesis 5 (Table 7). The global model at this scale was site type = structure + food + year + woodland + woodland \times structure + woodland \times food + year \times food, where tree structure included the same variables as for hypothesis 3. For the eight models considered at the patch scale, the direction and magnitude of the coefficients of all-variable models allowed us to assess hypothesis 4b (nest patches differ from non-nest patches in both food and structure), with the coefficients of all-variable models including interactions specifically addressing hypothesis 5 (Table 8). The global model at this scale was site type = structure + food + year + woodland + woodland \times structure + woodland \times food,

TABLE 7. Summary of rankings of all candidate models from multiple logistic regression assessing differences between *Phainopepla* nest trees and non-nest trees in 2002 and 2003 (hypotheses 4a and 5). “Structure” models include tree height (m), tree-crown diameter (m), percent cover within 5 m, and interactions of all three with woodland type if indicated; “food” models include berry abundance, berry abundance \times year, and berry abundance \times woodland type if indicated. “All” models include all structure and food variables, plus year, woodland type, and the above interactions as indicated. Models with interaction terms address hypothesis 5 directly. Models representing our predictions for this scale are italicized. The response variable was nest = 0, non-nest = 1. Sample size, n = 147 nest and 114 non-nest trees, K = number of parameters, w_i = Akaike weight.

Model	K	ΔAIC_c^a	w_i
<i>All (Structure + food + base + all interactions)^b</i>	12	0.00	0.90
All but year + year \times food	7	4.48	0.10
All but woodland + all woodland interactions with food and structure	7	14.28	0.00
<i>Structure + base + interactions with woodland</i>	9	14.96	0.00
All, no interactions	7	22.48	0.00
<i>Structure + base, no interactions</i>	6	42.37	0.00
Food + base + interactions with year and woodland	6	56.67	0.00
Food + base, no interactions	4	68.60	0.00
Year + woodland type (base model)	3	103.74	0.00

^aLowest AIC_c = 253.06

^bSee Table 5 for terms, coefficients, and standard errors of coefficients for this top model.

where patch structure included adjacent trees (m), number of trees 3–5 m high, and percent cover at the patch scale. We did not test the overall hypothesis of congruence between tree and patch scales (hypothesis 4) directly with a specific model but rather by comparing the model-selection results at the two scales. We considered that there was support for hypothesis 4 if the top models contained different combinations of variables at the two scales.

To reduce collinearity in our models, we included only variables with low pairwise correlations ($r^2 < 0.7$). If two variables were highly correlated, we chose the variable that best reflected our hypotheses and would be the best representative for that “factor” (i.e., food or structure) in our logistic-regression models. For example, the number of trees with berries in a patch was correlated with the number of trees with mistletoe; we chose the former as it more directly reflected our goal of assessing the role of food in nest-site selection. We analyzed data from 2002 and 2003 together; per Quinn and Keough (2002), before including both year and berry abundance in the same models, we ensured that the values of the latter were similar across the two levels of year (ANOVA: $F_{1,156} = 0.12$, $P = 0.73$). We performed all analyses with and without non-host nest trees. We used standardized normal values of all variables in analyses.

TABLE 8. Summary of rankings of all candidate models from multiple logistic regression assessing differences between Phainopepla nest patches and non-nest patches in 2002 and 2003 (hypotheses 4b and 5). "Structure" models include the variables mean distance to adjacent trees (m), number of trees 3–5 m high, percent cover at the patch scale, and interactions of the last two variables with woodland as indicated. "Food" models include the variables berry abundance of adjacent trees and number of trees with berries in the patch. "All" models include all structure and food variables, plus year, woodland type, and above interactions if indicated. Models with interaction terms address hypothesis 5. Models representing our predictions for this scale are italicized. The response variable was nest = 0, non-nest = 1. Sample size, $n = 137$ nest and 117 non-nest patches, K = number of parameters, w_i = Akaike weight.

Model	K	ΔAIC_c^a	w_i
<i>All (structure + food + base + woodland interactions with structure)^b</i>	10	0.00	0.76
<i>All but year</i>	9	2.33	0.24
Structure + base + interactions with woodland	8	33.98	0.00
<i>All but woodland + woodland interactions with structure</i>	7	39.45	0.00
<i>All, no interactions</i>	8	39.68	0.00
Structure + base, no interactions	6	61.24	0.00
Food + base, no interactions	5	69.84	0.00
Year + woodland type (base model)	3	110.79	0.00

^aLowest $AIC_c = 238.41$

^bSee Table 5 for terms, coefficients, and standard errors of coefficients for this top model.

RESULTS

GENERAL CHARACTERISTICS OF NESTS AND NEST TREES

We located 244 Phainopepla nests in 2001, 2002, and 2003, including 26 that were built but not used. In 2002, we identified 98 territories; 91 were held by pairs (as opposed to single males or females), but only 83 pairs (91%) initiated active nests. In 2003, we found 111 territories, and 101 pairs laid 100 clutches (99%). These results indicate that food (berries and insects) was sufficient for most individuals to initiate nesting in both years. Fifteen nests or nest trees were used in 2 years, and two nests were used all 3 years. Color banding revealed that, in at least one instance, the same nest was used by different individuals in subsequent years. Because we analyzed only active first nests, our sample consisted of 103 mesquite and 43 acacia nest trees and 96 mesquite and 41 acacia nest patches.

The first clutches were laid on 4 March 2002 and 9 February 2003, with mean clutch-initiation dates of March 31 (± 12.2 days) in 2002, and March 18 (± 19.6 days) in 2003. In 2001 we missed the first clutch at some sites so could not calculate the mean initiation date, but at least one nest was initiated by 10 March. The last days on which a nest was active were 6 June 2001, 25 May 2002, and 11 June 2003.

Most nests were in the two species of host trees (222 nests; 91%), but in mesquite study plots, 10 nests were in salt cedar (*Tamarix* spp.), four late-season nests were in cottonwoods (*Populus fremontii*), and one nest was in a young willow (*Salix* sp.) draped in wild grape (*Vitis* sp.). In acacia study plots, all but two nests, one in Mojave yucca (*Yucca schottii*) and one in desert willow (*Chilopsis linearis*), were in acacias. Outside our study areas, Phainopeplas nested in juniper (*Juniperus utahensis*; two nests), cholla (*Opuntia* spp.; two nests), desert oak (*Quercus turbinella*; three nests), and ash (*Fraxinus velutina*; one nest).

All but 15 host nest trees were infected by mistletoe. Of 165 first nests found in 2002 and 2003, 50% were hidden primarily by mistletoe and 46% were hidden primarily by branches (even when mistletoe was present). Cover around nests averaged $53.9 \pm 2.8\%$ in acacia and $54.2 \pm 3.6\%$ in mesquite, regardless of what material concealed nests.

In acacia sites, Phainopeplas nested significantly closer to the ground (158.0 ± 23.6 cm) than in mesquite sites (236.5 ± 9.3 cm, t -test $P = 0.01$), but, relative to total tree height, they nested higher in the tree (acacia: $65.9 \pm 9.0\%$ of tree height; mesquite: $51.3 \pm 6.9\%$ of tree height). Nests were built slightly closer to the trunk than to the edge of the canopy (distance from trunk/total distance = 0.45 ± 0.19 in acacia, 0.46 ± 0.23 in mesquite). In acacia, Phainopeplas had a significant preference for orienting their nests to the north and east (Pearson $\chi^2 = 7.8$, $df = 7$, $P = 0.013$). Phainopeplas nesting in mesquite showed no preference for nest orientation ($\chi^2 = 8.8$, $df = 7$, $P = 0.27$).

INSECT ABUNDANCE

Insect abundance did not differ significantly within ($F_{96,79} = 1.3$, $P = 0.14$) or among ($F_{7,24} = 0.89$, $P = 0.53$) sites or by year ($F_{1,3} = 4.18$, $P = 0.13$; repeated-measures ANOVA in PROC MIXED) (SAS 2005). Therefore it is unlikely to have affected nest-site selection.

NEST-SITE DIFFERENCES BETWEEN WOODLAND TYPES

Nest trees and patches differed by woodland type in both food and structure, as hypothesized. At the tree scale, all three top models contained both food and structure variables (Table 4). The best model ($w_i = 0.61$) contained all variables including year and year \times food, but the 95% confidence interval (CI) for the coefficient of year included 0 and two fairly competitive models ($\Delta AIC_c < 2.9$, $w_i = 0.25$ and 0.14 , respectively) did not include year or year \times food, so annual differences between nest trees in the two woodland types may be small. Food-only and structure-only models performed poorly ($\Delta AIC_c > 14$). In mesquite, nest trees were taller ($\beta = 1.90 \pm 0.64$; Fig. 2) and surrounded by more cover within 5 m than in acacia ($\beta = 2.77 \pm 0.62$; Table 3). Acacia nest trees had more berries than did mesquite nest trees ($\beta = -1.10 \pm 0.33$; Fig. 3).

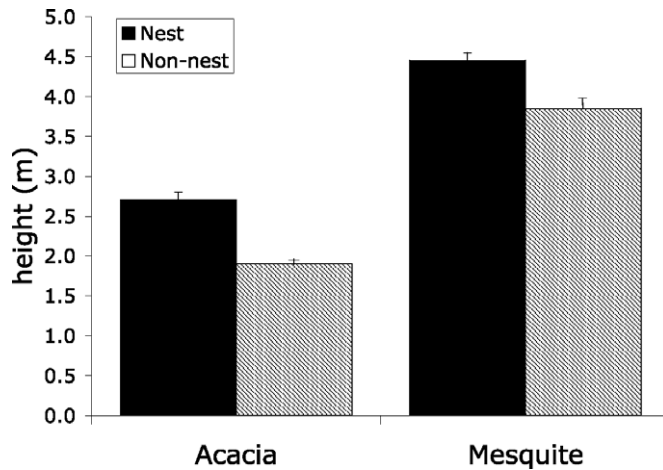


FIGURE 2. Height of *Phainopepla* nest trees ($n = 147$) and non-nest trees ($n = 114$) in six mesquite and two acacia woodlands in the Mojave Desert, 2002 and 2003.

Similarly, at the scale of the nest patch, the all-variable but year and all-variable models received much more support ($w_i = 0.76$ and 0.24 , respectively) than food-only and structure-only models ($\Delta AIC_c > 16$; Table 6). Nest patches in acacia appeared to contain more food, as represented by the number of berries on adjacent trees, than patches in mesquite, but the 95% confidence interval slightly overlapped zero ($\beta = -6.56 \pm 3.67$; Table 3). Trees in acacia nest patches appeared shorter than those in mesquite nest patches: there were slightly more trees in the 1- to 3-m category ($\beta = -31.1 \pm 17.5$) and fewer trees in the 3- to 5-m category ($\beta = 15.8 \pm 9.34$), and the mean height of adjacent trees was slightly lower ($\beta = 2.07 \pm 1.30$; all 95% CI contained 0). There was less cover in acacia nest patches than in mesquite nest patches ($\beta = 14.2 \pm 7.22$; 95% CI did not contain 0). Thus acacia nest sites seemed to have

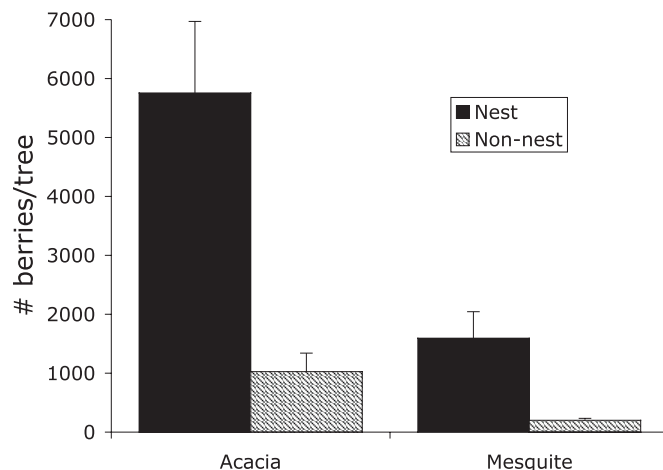


FIGURE 3. Abundance of mistletoe berries on *Phainopepla* nest trees ($n = 147$) and non-nest trees ($n = 114$) in six mesquite and two acacia woodlands in the Mojave Desert, 2002 and 2003.

more food and mesquite nest sites apparently had larger trees and more cover.

CONGRUENCE IN NEST-SITE SELECTION

Results of model selection indicated that the *Phainopepla*'s nest-habitat selection was congruent for food and structure at both the tree and patch scales, contrary to expectations (hypothesis 4), and incongruent between woodland types, as expected (hypothesis 5). At the tree scale, the model with all variables and interactions had stronger support ($w_i = 0.90$) than other models, which were >4 AIC_c units worse than the best model (Table 7). Food-only and structure-only models performed very poorly ($\Delta AIC_c > 14$, $w_i = 0.00$), while a model containing all variables except year and year \times food received moderate support ($\Delta AIC_c = 4.5$, $w_i = 0.10$). The presence of interactions in the top model supported the hypothesis that nest-site selection in the two woodland types differed (hypothesis 5). Collectively, these results indicated that *Phainopeplas* selected nest trees for both food and structure, but that the amount of food on, and structure of, nest trees vs. non-nest trees differed by woodland type. Nest trees were taller than non-nest trees ($\beta = -1.89 \pm 0.69$; Fig. 2), particularly in acacia, and were surrounded by more cover within a 5-m radius than non-nest trees ($\beta = -1.98 \pm 0.52$; Table 3). The number of berries was greater on nest trees than on non-nest trees ($\beta = -3.74 \pm 1.29$; Fig. 3), especially in mesquite. Finally, *Phainopeplas* in mesquite woodlands showed no preference for nesting in any of the three species of host trees (screwbean mesquite, honey mesquite, and acacia: $\chi^2 = 0.99$, $df = 2$, $P = 0.61$ in PROC FREQ, SAS 2005).

As predicted at the patch scale, strong support for the all-variable model with interactions ($w_i = 0.76$) and modest support for the all-variable-but-year-model ($\Delta AIC_c = 2.3$, $w_i = 0.24$; Table 8) suggested that *Phainopeplas* selected nest patches for both vegetation structure and food, the latter especially in mesquite woodlands. The interactions in top models supported our hypothesis 5 that nest-site selection in the two types of woodland was incongruent in some features. There was no support for food-only or structure-only models ($\Delta AIC_c > 30$). Trees adjacent to nest trees were slightly closer ($\beta = -0.42 \pm 0.20$) and had more berries ($\beta = -1.12 \pm 0.31$) than trees next to non-nest trees, especially in mesquite (Table 8). In both woodland types, nest patches had more host trees with berries than did non-nest patches ($\beta = -1.49 \pm 0.35$). Host trees 3–5 m tall were more numerous in nest patches than in non-nest patches ($\beta = -4.55 \pm 0.98$), especially in acacia.

In summary, nest-site selection was congruent across both the tree and patch scales, contrary to expectations. At both scales, nest sites contained more food and tall trees than did non-nest sites. While nest sites were selected for both food and structure in both woodland types, selection was incongruent with respect to relative food abundance, size, density, and cover in the two woodland types, as expected.

DISCUSSION

Phainopeplas demonstrated an unexpectedly high degree of congruence in nest-site selection across scales, responding to both vegetation structure and food abundance at the nest and patch scales within woodland types; apparently most birds maximized both attributes rather than trading off one for the other. They preferred nest trees that were taller, wider, and had more cover and mistletoe berries than non-nest trees, and they preferred nest patches that had taller trees, higher density of host trees, and more berries than did non-nest patches, regardless of woodland type. This congruence underscores the importance of these attributes to breeding Phainopeplas and suggests that benefits of selecting both food and vegetation structure outweigh the disadvantages of foraging close to the nest, such as attracting predators (Martin et al. 2000). However, Phainopeplas apparently compensated for differences between woodland types by choosing relatively taller trees in acacia and relatively food-rich sites in mesquite, leading to less congruence between types, as we had predicted.

The congruence between scales was unexpected; we had predicted that food abundance would not be selected at the nest-tree scale for two reasons. First, foraging at the nest might attract predators (Martin et al. 2000). Second, food (berry or insect) abundance was not correlated with nest survival at this scale (Crampton 2004). Indeed, insect abundance likely was not a factor in nest-site selection at any scale, as we did not find it to differ within or among sites or years. However, Phainopeplas selected both nest trees and patches with high berry abundance, which is correlated with other measures of the species' reproductive success (e.g., density of breeding pairs, clutch size; Walsberg 1977, Chu and Walsberg 1999). All measures of berry abundance (the number of berries on nest trees and adjacent trees, the number of host trees that had mistletoe with berries) were greater on and around nest trees than non-nest trees.

This congruence may reflect one or more processes. In acacia, berry abundance, mistletoe volume (which adds to cover), and tree height are moderately correlated ($r^2 = 0.53\text{--}0.60$), so selection of vegetation structure and food often may be inseparable, which would favor congruence across scales. At our more numerous mesquite nest sites, where these three habitat elements were only weakly correlated ($r^2 = 0.02\text{--}0.29$) and berries were less abundant, congruence may have been promoted by a need to increase berries in the territory by selecting nest trees with abundant berries. Similarly, in Pennsylvania Red-eyed Vireos (*Vireo olivaceus*) select nest sites around which the amount of their preferred foraging substrate is greater (Siepielski et al. 2001). Both species may anticipate requirements of nestlings and select only nest sites that have food sufficient to satisfy those needs. Close proximity of food favors frequent provisioning of nestlings. Despite potential risks of attracting predators, foraging in nest sites with abundant food may facilitate participation of the foraging parent(s)

in territory and nest defense. Phainopeplas attend nests frequently and respond aggressively to predators, including accipiters, and to hetero- and conspecific competitors (Chu and Walsberg 1999, Crampton et al. 2004).

As expected, at all scales Phainopeplas used nest sites with vegetation structure that may reduce predation, the major cause of their nests' failure (Crampton 2004), and thermoregulatory stress. At the nest scale, Phainopeplas nested near the vertical and horizontal center of mesquite trees; in shorter acacia trees, they nested slightly higher relative to total tree height. This placement may be a compromise to avoid predation from both ground and aerial predators while simultaneously reducing overheating from the sun. Thus mid-tree nest placement may improve nest success, as observed for Eastern Kingbird (*Tyrannus tyrannus*) nests in Kansas and New York (Murphy 1983). The frequent placement of nests in or under large, dense mistletoes also may have mitigated aerial predation and overheating. The preference for the north and east sides of acacias (which do not leaf out until the end of the breeding season) may allow Phainopeplas to warm up in early morning sun while avoiding overheating in the afternoon.

At the tree and patch scales, Phainopeplas selected tall, wide trees and more cover. Similarly, in central Texas Black-capped Vireos (*Vireo atricapilla*) also select tall trees with high foliage cover as nest sites, but since their nest success has not been evaluated the fitness implications of such nest sites are not clear (Bailey and Thompson 2007). Phainopeplas often use tall trees for territorial advertisement (Aukema 2001), flycatching insects, or nest defense (LHC, pers. obs.). Predators' efficiency of searching may decrease in large trees because there are more sites to investigate (Martin and Roper 1988), which may explain why tree height was more important to habitat selection in shorter acacia. Predation risk also may be lower in dense cover (Martin and Roper 1988, Liebezeit and George 2002), perhaps because cover reduces olfactory and visual cues to predators (Holway 1991, Martin 1993) or predators' efficiency of searching (Martin 1993). Furthermore, for sparrows and warblers, dense cover has been linked to improved thermoregulation (Holway 1991, Lusk et al. 2003).

In our study and in southern Arizona (Powell and Steidl 2002), the Phainopepla selected nest patches with a density of trees higher than that of non-nest patches. Similar selection of nest sites with a high density of saplings by the Rose-breasted Grosbeak (*Pheucticus ludovicianus*) in southern Ontario was correlated higher nest success (Smith et al. 2007). High tree density may reduce predation risk, perhaps because a profusion of potential nest trees hampers predators' search efficiency (Martin and Roper 1988, Smith et al. 2007). However, Eastern Kingbirds in New York (Murphy et al. 1997) and Dusky Flycatchers (*Empidonax oberholseri*; Liebezeit and George 2002) in northeastern California have higher nest success in sparsely vegetated patches. This inconsistency in the effect of tree density on nest survival may be result from

interspecific differences in nest-defense strategies or nest predators' behavior. For example, Dusky Flycatcher nests in sparse vegetation are more susceptible to avian than to mammalian predation (Liebezeit and George 2002). Differences between mesquite and acacia sites in their suite of predators (Forstmeier and Weiss 2004) and nest-patch structure may explain the interaction we found between density of infected trees and woodland type in the Phainopepla's nest-site selection.

Given that predation is a major cause of nest failure but that Phainopeplas do not nest if food is scarce (Walsberg 1977, Chu and Walsberg 1999), much of nest-site selection is likely an attempt to enhance nest success by maximizing nest safety, thermoregulatory conditions, and foraging opportunities. Although other studies (e.g., Holway 1991, Murphy et al. 1997, Siepielksi et al. 2001, Liebezeit and George 2002), have found that in passerines nest-site selection and nest success are not always clearly linked, all the food and structure variables that predict the Phainopepla's nest success at multiple spatial scales were involved in nest-site selection (Crampton 2004). Perhaps these other studies did not examine relevant variables, such as food abundance, or appropriate spatial or temporal scales. Alternatively, perhaps selected nest attributes influence other aspects of reproductive success (e.g., nest initiation, social interactions) or strongly affect nest survival elsewhere in the species' range, where the suite of predators or thermoregulatory environment may differ. In that vein, Phainopeplas also selected some nest-site features (e.g., number of tall trees, percent cover in the nest patch) that do not directly or strongly influence nest survival at our study sites (Crampton 2004).

Most studies of passerines have examined nest-site selection only in a single woodland type, so they have been unable to draw conclusions about congruence between woodland types as we did (but see Sakai and Noon 1991, Luck 2002, Saab et al. 2009, Smith et al. 2009). In our study, the lack of congruence in nest sites in the two woodland types indicates that nesting Phainopeplas can adjust to variation in vegetation structure and food abundance; this possibility should be investigated experimentally. Interestingly, the Phainopepla's nest-site selection is also incongruent with its selection of woodlands at the landscape (among-patch) level; across multiple (65) mesquite and acacia woodlands, wintering and breeding Phainopeplas responded strongly only to food abundance, not to vegetation structure (Crampton et al. 2011). Apparently, at larger spatial scales only food abundance is important to habitat selection, whereas both food abundance and vegetation structure are important at small, within-patch spatial scales, such as the nest-site scales we studied. Vegetation structure may also play a role at larger within-patch scales (e.g., territory) that we have not examined. In a small study of territory (within-patch) selection at two acacia sites, Phainopeplas preferred areas of tall trees with abundant berries (Liang 2004). This result reinforces our finding that the Phainopepla's habitat selection is congruent for both vegetation structure

and food across within-patch scales but is incongruent at the among-patch scale, where only food is important. To verify this conclusion, the territory (and any other relevant within-woodland) scale should be studied further in a wider range of woodlands.

As have other studies (McLoughlin et al. 2002, 2004, Morin et al. 2005, Barg et al. 2006), our consideration of multiple factors and a hierarchy of smaller spatial scales revealed the importance of some habitat features that would have been overlooked had we examined only the landscape scale (e.g., the scale studied by Crampton et al. 2011) or one factor. Although the abundance of foraging sites may be a factor in some species' selection of breeding habitat (e.g., Holway 1991, Siepielski et al. 2001), food abundance rarely is measured and accounted for in investigations of habitat selection. This study underscored its importance in selection of breeding habitat across several spatial scales, as food abundance strongly influenced selection of nest trees and patches, especially in mesquite where berries are less abundant. Yet vegetation structure was also clearly important to selection of nesting habitat at all scales we considered. Jointly, these results suggest that strategies for Phainopepla management should preserve habitat patches with a high density of large trees and abundant mistletoe berries so that Phainopeplas can continue to find nest sites with both abundant food and suitable vegetation structure. As importantly, they highlight the importance of considering multiple hypotheses and spatial scales in studies of breeding-habitat selection. Animals may select habitat on the basis of different factors at different scales, may select habitat that allows several features to be optimized simultaneously, or may select habitat that minimizes tradeoffs between various attributes.

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LITERATURE CITED

- AUKEMA, J. E. 2001. Dispersal and spatial distribution of the desert mistletoe, *Phoradendron californicum*, at multiple scales: patterns, processes and mechanisms. Ph. D. dissertation. University of Arizona, Tucson, AZ.
- AUSTIN, G. T. 1974. Nesting success of the Cactus Wren in relation to nest orientation. *Condor* 76:216–217.
- BAILEY, J. W., AND F. R. THOMPSON. 2007. Multiscale nest-site selection by Black-capped Vireos. *Journal of Wildlife Management* 71:828–836.
- BARG, J. J., D. M. AIAMA, J. JONES, AND R. J. ROBERTSON. 2006. Within-territory habitat use and microhabitat-selection by male Cerulean Warblers (*Dendroica cerulea*). *Auk* 123:795–806.

- BISSONETTE, J. A., D. J. HARRISON, AND C. D. HARGIS. 1997. The influence of spatial scale and scale-sensitive properties in habitat selection by American marten, p. 368–385. *In* J. A. Bissonette [ED.], *Wildlife and landscape ecology: effects of pattern and scale*. Springer, New York.
- BLM. 1998. Memorandum NV-98-013. Bureau of Land Management, Las Vegas, NV.
- BURNHAM, K. P., AND D. R. ANDERSON. 2002. *Model selection and multimodel inference*, 2nd edition. Springer-Verlag, New York.
- CAMERON, M., AND R. B. CUNNINGHAM. 2006. Habitat selection at multiple spatial scales by foraging Glossy Black-Cockatoos. *Austral Ecology* 31:597–607.
- CHU, M. C., AND G. E. WALSBERG. 1999. Phainopepla (*Phainopepla nitens*), no. 415. *In* A. Poole and F. Gill [EDS.], *The birds of North America*. Birds of North America, Inc., Philadelphia.
- CRAMPTON, L. H. 2004. Ecological determinants of Phainopepla (*Phainopepla nitens*) abundance and breeding success in the northeastern Mojave Desert. Ph.D. dissertation, University of Nevada, Reno.
- CRAMPTON, L. H., H. T. LIANG, AND L. GREENE. 2004. First records of predation by coachwhip snakes (*Mastocophis flagellum*) on nests of Phainopeplas (*Phainopepla nitens*). *Great Basin Birds* 7:34–39.
- CRAMPTON, L. H., W. S. LONGLAND, D. D. MURPHY, AND J. S. SEDINGER. 2011. Food abundance determines distribution and density of a frugivorous bird across seasons. *Oikos* 120:65–76.
- DORAN, P. J., AND R. T. HOLMES. 2005. Habitat occupancy patterns of a forest dwelling songbird: causes and consequences. *Canadian Journal of Zoology* 83:1297–1305.
- FORSTMIEIER, W., AND I. WEISS. 2004. Adaptive plasticity in nest-site selection in response to changing predation risk. *Oikos* 104:487–499.
- HILDEN, O. 1965. Habitat selection in birds. *Annales Zoologici Fennici* 2:53–75.
- HOLWAY, D. A. 1991. Nest-site selection and the importance of nest concealment in the Black-throated Blue Warbler. *Condor* 93:575–581.
- HOSMER, D., AND S. LEMESHOW. 2003. *Applied logistic regression*, 2nd edition. Wiley, New York.
- HOWE, F. P., R. L. KNIGHT, L. C. MCEWEN, AND T. L. GEORGE. 1996. Direct and indirect effects of insecticide applications on growth and survival of nestling passerines. *Ecological Applications* 6:1314–1324.
- HUTTO, R. L. 1985. Habitat selection by nonbreeding, migratory landbirds, p. 455–476. *In* M. L. Cody [ED.], *Habitat selection in birds*. Academic Press, London.
- JANSEN, R., E. R. ROBINSON, R. M. LITTLE, AND T. M. CROWE. 2001. Habitat constraints limit the distribution and population density of Redwing Francolin, *Francolinus levaillantii*, in the highland grasslands of Mpumalanga province, South Africa. *African Journal of Ecology* 39:146–155.
- JENKINS, D. A., J. A. SCHAEFER, R. ROSATTE, T. BELLHOUSE, J. HAMR, AND F. F. MALLORY. 2007. Winter resource selection of reintroduced elk and sympatric white-tailed deer at multiple spatial scales. *Journal of Mammalogy* 88:614–624.
- JOHNSON, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61:65–71.
- KOTLIAR, N. B., AND J. A. WIENS. 1990. Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. *Oikos* 59:253–260.
- KRISTAN, W. B., M. D. JOHNSON, AND J. T. ROTENBERRY. 2007. Choices and consequences of habitat selection for birds. *Condor* 109:485–488.
- KRUEGER, J. B. 1998. Use of mesquite woodlands in southern Nevada as breeding habitat for Phainopepla (*Phainopepla nitens*). *Great Basin Birds* 1:59–60.
- KWIT, C., D. J. LEVEY, C. H. GREENBERG, S. F. PEARSON, J. P. MCCARTY, S. SARGENT, AND R. L. MUMME. 2004. Fruit abundance and local distribution of wintering Hermit Thrushes (*Catharus guttatus*) and Yellow-rumped Warblers (*Dendroica coronata*) in South Carolina. *Auk* 121:46–57.
- LENNINGTON, S. 1980. Female choice and polygyny in Red-winged Blackbirds. *Animal Behaviour* 28:347–361.
- LIANG, H. T. 2004. Nest ecology of Phainopepla (*Phainopepla nitens*) in southern Nevada. M.Sc. thesis, University of Nevada, Las Vegas, NV.
- LIEBEZEIT, J. R., AND T. L. GEORGE. 2002. Nest predators, nest-site selection, and nesting success of the Dusky Flycatcher in a managed ponderosa pine forest. *Condor* 104:507–517.
- LUCK, G. W. 2002. The habitat requirements of the Rufous Treecreeper (*Climacteris rufa*). 1. Preferential habitat use demonstrated at multiple spatial scales. *Biological Conservation* 105:383–394.
- LUSK, J. J., K. S. WELLS, F. S. GUTHERY, AND S. D. FUHLENDORF. 2003. Lark Sparrow (*Chondestes grammacus*) nest-site selection and success in a mixed-grass prairie. *Auk* 120:120–129.
- MARTIN, T. E. 1987. Food as a limit on breeding birds: a life-history perspective. *Annual Review of Ecology and Systematics* 18:453–487.
- MARTIN, T. E. 1993. Nest predation and nest sites—new perspectives on old patterns. *BioScience* 43:523–532.
- MARTIN, T. E., AND G. R. GEUPEL. 1993. Nest-monitoring plots: methods for locating nests and monitoring success. *Journal of Field Ornithology* 64:507–519.
- MARTIN, T. E., AND P. J. LI. 1992. Life-history traits of open-nesting vs cavity-nesting birds. *Ecology* 73:579–592.
- MARTIN, T. E., AND J. J. ROPER. 1988. Nest predation and nest-site selection of a western population of the Hermit Thrush. *Condor* 90:51–57.
- MARTIN, T. E., J. SCOTT, AND C. MENGE. 2000. Nest predation increases with parental activity: separating nest site and parental activity effects. *Proceedings of the Royal Society of London B* 267:2287–2293.
- McLOUGHLIN, P. D., R. L. CASE, R. J. GAU, H. D. CLUFF, R. MULDER, AND F. MESSIER. 2002. Hierarchical habitat selection by barren-ground grizzly bears in the central Canadian Arctic. *Oecologia* 132:102–108.
- McLOUGHLIN, P. D., L. R. WALTON, H. D. CLUFF, P. C. PAQUET, AND M. A. RAMSAY. 2004. Hierarchical habitat selection by tundra wolves. *Journal of Mammalogy* 85:576–580.
- MORIN, P., D. BERTEAUX, AND I. KLVANA. 2005. Hierarchical habitat selection by North American porcupines in southern boreal forest. *Canadian Journal of Zoology* 83:1333–1342.
- MURPHY, M. T. 1983. Nest success and nesting habits of Eastern Kingbirds and other flycatchers. *Condor* 85:208–219.
- MURPHY, M. T., C. L. CUMMINGS, AND M. S. PALMER. 1997. Comparative analysis of habitat selection, nest site and nest success of Cedar Waxwings (*Bombycilla cedrorum*) and Eastern Kingbirds (*Tyrannus tyrannus*). *American Midland Naturalist* 138:344–356.
- MYSTERUD, A., P. K. LARSEN, R. A. IMS, AND E. OSTBYE. 1999. Habitat selection by roe deer and sheep: does habitat ranking reflect resource availability? *Canadian Journal of Zoology* 77:776–783.
- ORIAN, G. H., AND J. F. WITTENBERGER. 1991. Spatial and temporal scales in habitat selection. *American Naturalist* 137:S29–S49.
- POWELL, B. F., AND R. J. STEIDL. 2002. Habitat selection by riparian songbirds breeding in southern Arizona. *Journal of Wildlife Management* 66:1096–1103.

- QUINN, G. P., AND KEOUGH, M. J. 2002. Experimental design and data analysis for biologists. Cambridge University, Cambridge, England.
- Recon. 2000. Clark County Multiple Species Habitat Conservation Plan and environmental impact assessment. Clark County, Las Vegas, NV.
- RETTIE, W. J., AND F. MESSIER. 2000. Hierarchical habitat selection by woodland caribou: its relationship to limiting factors. *Ecography* 23:466–478.
- RICKLEFS, R. E. 1969. An analysis of nesting mortality in birds. *Smithsonian Contributions to Zoology* 9.
- RODEWALD, P. G., AND M. C. BRITTINGHAM. 2007. Stopover habitat use by spring migrant landbirds: the roles of habitat structure, leaf development, and food availability. *Auk* 124:1063–1074.
- SAAB, V. A., R. E. RUSSELL, AND J. G. DUDLEY. 2009. Nest-site selection by cavity-nesting birds in relation to postfire salvage logging. *Forest Ecology and Management* 257:151–159.
- SAKAI, H. F., AND B. R. NOON. 1991. Nest-site characteristics of Hammond's and Pacific-slope flycatchers in northwestern California. *Condor* 93:563–574.
- SAS. 2001. Version 8.3. SAS Institute, Cary, NC.
- SAS. 2005. Version 9.1. SAS Institute, Cary, NC.
- SAUER, J. R., J. E. HINES, AND J. FALLON. 2005. The North American Breeding Bird Survey, results and analysis, 1966–2002. U.S. Geological Survey Patuxent Wildlife Research Center, Laurel, MD.
- SCHAEFER, J. A., AND F. MESSIER. 1995. Habitat selection as a hierarchy: the spatial scales of winter foraging by muskoxen. *Ecography* 18:333–344.
- SEDGWICK, J. A., AND F. L. KNOPF. 1992. Describing Willow Flycatcher habitats: scale perspectives and gender differences. *Condor* 94:720–733.
- SIEPIELSKI, A. M., A. D. RODEWALD, AND R. H. YAHNER. 2001. Nest site selection and nesting success of the Red-eyed Vireo in central Pennsylvania. *Wilson Bulletin* 113:302–307.
- SIMONS, L. S., AND T. E. MARTIN. 1990. Food limitation of avian reproduction—an experiment with the Cactus Wren. *Ecology* 71:869–876.
- SMITH, D. M., D. M. FINCH, AND D. L. HAWKSWORTH. 2009. Black-chinned Hummingbird nest-site selection and nest survival in response to fuel reduction in a southwestern riparian forest. *Condor* 111:641–652.
- SMITH, L. A., E. NOL, D. M. BURKE, AND K. A. ELLIOTT. 2007. Nest-site selection of Rose-breasted Grosbeaks in southern Ontario. *Wilson Journal of Ornithology* 119:151–161.
- WALSBERG, G. 1977. Ecology and energetics of contrasting social systems in *Phainopepla nitens* (Aves: Ptilonotidae). *University of California Publications in Zoology* 108:1–61.
- WALSBERG, G. E. 1981. Nest-site selection and the radiative environment of the Warbling Vireo. *Condor* 83:86–88.