1	Behavior-specific occupancy patterns of Pinyon Jays (Gymnorhinus
2	cyanocephalus) in three Great Basin study areas and significance for
3	pinyon-juniper woodland management
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5	(Short Title): Behavior-specific Pinyon Jay occupancy patterns
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13 **Abstract** (Level 1 heading)

The Pinyon Jay is a highly-social, year-round inhabitant of pinyon-juniper woodlands in the 14 western United States. Range-wide, Pinyon Jays have declined $\sim 3 - 4\%$ per year for at least the 15 last half-century. At the same time, large acreages of pinyon-juniper woodland have been 16 17 removed or thinned to improve habitat for Greater Sage-Grouse or other game species across 18 much of the Great Basin, which is home to nearly half of the global population of Pinyon Jays. 19 Occupancy patterns and habitat use of Pinyon Jays have not been well characterized across much 20 of the species' range, and obtaining this information is necessary for better understanding the 21 causes of ongoing declines and determining useful conservation strategies. Our goal of this study 22 was to identify the characteristics of areas used by Pinyon Jays for several critical life history 23 components and to thereby facilitate the inclusion of Pinyon Jay conservation measures in the design of vegetation management projects. To accomplish this, we studied Pinyon Jays in three 24 25 widely separated study areas using radio telemetry and direct observation, and measured key attributes of their locations and a separate set of randomly-selected control sites using the U.S. 26 27 Forest Service's Forest Inventory Analysis protocol. Data visualizations, non-metric dimension 28 scaling ordinations, and logistic regressions of the resulting data indicated that Pinyon Jay occupancy was concentrated in a distinct subset of available pinyon-juniper woodland habitat, 29 30 and further that Pinyon Jays used different habitats, arrayed along elevational and tree-cover 31 gradients, for seed caching, foraging, and nesting. Caching was concentrated in low-elevation, relatively flat areas with low tree cover; foraging occurred at slightly higher elevations with 32 moderate tree cover, and nesting was concentrated in somewhat higher areas with greater tree 33 cover and higher stand density. All three of these Pinyon Jay behavior types were highly 34 concentrated within the lower-elevation band of pinyon-juniper woodland close to the woodland-35

36	shrubland ecotone. Because woodland removal projects in the Great Basin are often concentrated
37	in these same areas, it is critical to incorporate conservation measures informed by Pinyon Jay
38	occupancy patterns into existing woodland management paradigms, protocols, and practices.
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41	Introduction (level 1 heading)

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The Pinyon Jay (*Gymnorhinus cyanocephalus*) is a highly-social corvid that inhabits pinyon-43 44 juniper and other coniferous woodlands in the interior western U. S. [1-3] (Fig 1). Pinyon Jays form year-round flocks that can range from a few dozens to several hundred members [3-6]. 45 They are perhaps best known for harvesting and caching the seeds, or "pine nuts", of the pinyon 46 pine (primarily *Pinus monophylla* and *P. edulis*) as their primary food source, though they also 47 consume other conifer seeds and insects [3, 7, 8]. Pinyon Jays are present year-round in parts of 48 at least ten states, but most of their range lies within Bird Conservation Regions (BCRs) 9 49 ("Great Basin") and 16 ("Southern Rockies and California Plateau") [9], with highest densities in 50 51 central-eastern Nevada and western New Mexico (Fig 2). Since North American Breeding Bird Survey data collection began in 1967, Pinyon Jays have experienced steep and sustained declines 52 averaging 3-4% per year both range-wide and within most of the states and regions they occupy 53 [4, 10]. This equates to a loss of about 85% of the population over 50 years, one of the largest 54 55 recorded declines among all widely-distributed passerine birds in the interior western United States [10, 11]. 56

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Fig 1. Distribution of the Pinyon Jay [4], pinyon pine (Pinus monophylla and P. edulis 58 combined), and juniper (Juniperus osteosperma, J. occidentalis, and J. spoculorum 59 combined) [5]. Some of the juniper distribution is invisible under the pinyon pine 60 distribution on the map. 61 62 63 Fig 2. Relative density of the Pinyon Jay (purple colors, with darker colors representing higher relative densities [4]) and Bird Conservation Regions (BCRs) 9 (Great Basin) and 16 64 65 (Southern Rockies / Colorado Plateau). 66 Despite this decline, no systematic conservation efforts have been undertaken for the Pinyon Jay, 67 although it is included on the 'sensitive species' lists of many federal and state management 68 69 agencies and avian conservation organizations [12-15], and is the subject of a recent interagency working group conservation strategy [15]. The lack of conservation action for Pinyon Jays may 70 be attributable to several factors. First, despite a rich knowledge of the species' social behavior, 71 breeding behavior, and spatial memory [6, 16, 17], its occupancy and habitat use patterns are 72 poorly characterized and understudied in most parts of its range. Second, there are no widely-73 74 accepted or strongly-supported hypotheses about the causes of Pinyon Jay population declines. Finally, the landscapes inhabited by Pinyon Jays are primarily managed for other priorities. 75 These include improving habitat for game species such as Greater Sage-Grouse (Centrocercus 76 77 *urophasianus*) and mule deer (*Odocoileus heminus*), creating wildlife corridors, and mitigating fire hazards [3, 18-22]. 78 79

Pinyon Jay declines could be related, at least in part, to changes in the pinyon-juniper woodlands 80 that comprise most of their habitat [3, 22-24] and much of the forested landscape of the Great 81 Basin (i.e., BCR 9) and Colorado Plateau (i.e., BCR 16) [25-28]. The spatial extent of pinvon-82 juniper woodlands (most commonly a Pinus monophylla - Juniperus osteosperma association) in 83 84 this region has undergone climate-induced fluctuations since the end of the Pleistocene epoch 85 11,500 years ago [29, 30], but it has been suggested by some authors that over the last 150 years, extension of local woodland range (i.e. "expansion") and increased tree densities within extant 86 stands (i.e. "infill") have occurred at atypical and perhaps unprecedented rates, at least in the 87 88 Great Basin [22, 31-34]. Other authors have questioned this conclusion and suggest that expansion and infill are either localized, part of a historically normal pattern of spatio-temporal 89 90 woodland dynamics, or represent recoveries from earlier widespread clearing during the western 91 settlement period [22, 35, 36]. Regardless of which of these paradigms is correct, over recent decades extensive acreages of pinyon-juniper woodlands have been clear cut or thinned by 92 93 resource management agencies and private owners to accomplish various management objectives 94 [3, 37, 38].

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In the Great Basin, the primary pinyon-juniper woodland management objective over the last 20
years has been creation or restoration of shrubland habitat by clear cutting stands that are
regarded as encroaching into shrublands, often with a goal of benefitting Greater Sage-Grouse
[39, 40]. If and how this type of vegetation management affects Pinyon Jays remains
undetermined. Answering this question requires a better understanding of Pinyon Jay occupancy
patterns and habitat use in the Great Basin, determining the extent of overlap between their
preferred habitats and ongoing vegetation management activities, and monitoring or modeling

103	the effects of those activities. In this study, we compared the habitats used by Pinyon Jays for
104	caching or retrieving seeds, for foraging, and for nesting, to the full range of habitat available
105	within pinyon-juniper woodlands. Our goals were to determine whether Pinyon Jays in the Great
106	Basin used predictable subsets of available habitat for these distinct behavior types. If so, this
107	information could assist managers seeking to incorporate Pinyon Jay conservation measures into
108	existing vegetation management programs for pinyon-juniper woodlands, and help to guide
109	future research [15].
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112	Methods (level 1 heading)
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	Overview of study design and study region (level 2 heading)
114	Overview of study design and study region (level 2 heading)
115	
116	We used a case-control study design [41, 42], with observed locations of Pinyon Jay flocks as
117	case records and a set of pre-existing Forest Inventory Analysis (FIA) plots established by the
118	U.S. Forest Service (USFS) as control sites (see below for details). Pinyon Jay data were
119	collected from 2008 – 2014 in three Great Basin study areas. The control sites were distributed
120	over a broader study region located entirely within the Central Basin and Range Ecoregion [43]
121	and BCR 9 (Fig 2) that encompassed all three Pinyon Jay study areas (Fig 3). Control sites were
122	not assumed to be unoccupied by Pinyon Jays, but were intended to provide a representative
123	characterization of the diversity of pinyon-juniper woodland habitat available within the general
124	study region. Habitat at Pinyon Jay locations and control sites was quantified using the
125	standardized FIA protocol (see below) within circular 0.405-ha (1-acre) plots, which defined the

126	spatial scale of this analysis. Analyses consisted of ordinations and logistic regressions,
127	supplemented by data visualizations. We recognize the potential bias inherent in case-control
128	sampling designs and followed Manly et al.'s [44] and Keating and Cherry's [42] guidance for
129	analysis.
130	
131	Fig 3. Locations of three Pinyon Jay study areas and FIA plots that served as control sites.
132	FIA plot locations are approximate (i.e. "fuzzed") to comply with USFS data protection
133	policies. FIA plots are color coded to indicate the Pinyon Jay study area with which they
134	were analytically paired.
135	
136	Pinyon Jay study areas and timeline (level 2 heading)
137	
138	Pinyon Jay locations came from multiple Pinyon Jay flocks in these three study areas (Fig 3):
139	1) Eastern Nevada (~ 63,130-ha study area), specifically the foothills between Baker,
140	Nevada and Great Basin National Park, and Steptoe Valley south of the town of Ely,
141	Nevada. This area is mostly comprised of public lands managed by the U.S. Bureau of
142	Land Management, but includes some private property near Baker. Pinyon Jay data were
143	collected from $2/28/2008 - 6/26/2008$ and from $5/10/2009 - 8/27/2009$.
144	2) Southern Idaho (~ 23,470-ha study area), specifically the area in and around City of
145	Rocks National Reserve and Castle Rocks State Park in Cassia County. This study area
146	contains the northernmost occurrence of pinyon pine in North America [45]. Jurisdictions
147	within the study area are the U.S. National Park Service, Idaho State Parks, U.S. Bureau

148	of Land Management, and private lands. Pinyon Jay data were collected from 7/20/2012
149	-10/5/2012.

150	3) <u>Central Nevada (~ 89,030-ha study area)</u> , specifically the Desatoya Range which lies
151	along the border between Churchill County on the west and Lander County on east. This
152	study area is comprised almost exclusively of U.S. Bureau of Land Management lands,
153	with limited private inholdings. Pinyon Jay data were collected from 3/29/2013 -
154	6/5/2013.

155

156 Study area locations and periods of data collection were governed by three different funding agreements, and therefore seasonality was not standardized across all three areas. All study areas 157 are characterized by mountainous "basin and range" topography, with plant communities 158 159 dominated by big sagebrush (Artemisia tridentata) at lower elevations, pinyon-juniper woodlands at mid-elevations, and various mountain shrub and forest types at high elevations. 160 Pinyon-juniper woodlands range in elevation from $\sim 1,500 \text{ m} - 2,600 \text{ m}$ across all study areas, 161 and are usually comprised of varying proportions of *P. monophylla* and *J. osteosperma*. Public 162 lands in all study areas are managed for multiple uses and experience varying levels of livestock 163 grazing and off-road vehicle travel. 164

165

Pinyon Jay data collection and processing (level 2 heading)

167

Pinyon Jay data collection had several distinct components; initial searches, observational
surveys, capture and radio-tagging, and radio-telemetry surveys. The observational surveys and
radio-telemetry surveys generated the Pinyon Jay locations that are the basis of our analyses.

171

172	Initial searches of potential Pinyon Jay habitat (defined as pinyon-juniper woodlands and
173	visually adjacent shrublands) were conducted during the first 1-2 weeks of field work at a given
174	study area on foot and by vehicle to identify all or most of the Pinyon Jay flocks present.
175	Because Pinyon Jay flocks are visually apparent from long distances, "noisy" (except when at
176	the nest), and spatially segregated from one another, we regarded this a feasible goal. Search
177	patterns used during initial searches were not systematized but were instead tailored to take
178	advantage of local topography and access points. Areas searched were delineated on imagery
179	maps to facilitate thorough coverage of pinyon-juniper woodland across a given study area.
180	Upon detecting a flock, the observer usually maintained contact over a period of 1-3 h on each of
181	several visits to obtain a preliminary and approximate delineation of the flock's movement
182	patterns and primary activity areas.

183

Flocks that were consistently detected during initial searches were then subjected to more 184 intensive study by observational surveys and/or radio-telemetry surveys to obtain a sample of 185 occupied locations. Observational surveys involved establishing visual contact with a flock; 186 observing the flock with binoculars from a distance sufficient to prevent alteration of flock 187 behavior (typically > 75 m); and recording approximately once per hour the point coordinates of 188 the estimated centroid of the flock's location along with estimated flock size and predominate 189 190 behavior type (Table 1) whenever possible. The goal of observational surveys was to obtain locations across an entire daylight cycle at least once per week (usually assembled from several 191 observation sessions conducted during different time periods on different days) for each flock 192 193 over the duration of the data collection period. Coordinates of flocks were usually obtained by

194	recording observer position with a GPS unit; recording a bearing to the visually-estimated flock
195	centroid with a compass; measuring distance to the flock centroid by rangefinder or estimating
196	distance by eye (for shorter distances < 25 m); and then plotting the flock's estimated point
197	location in GIS based on these parameters. In some cases, coordinates could be obtained directly
198	by GPS after a flock vacated a previously-occupied location. As observers became increasingly
199	familiar with the daily movement patterns of a flock, which tended to be consistent, their efforts
200	were increasingly focused on the portions of the daily activity cycle that were more difficult to

201 characterize.

202

Behavior Type	Description
Caching	Birds observed either caching or retrieving previously-cached pine
	nuts or other similar food items.
Foraging	Birds observed collecting any type of new food item in trees, shrubs,
	or on the ground, including pinyon nuts, other plant material, or
	insects.
Nesting	Nest site or sites confirmed by direct observation or by confirmatory
	behaviors, such as carrying nest materials.
Roosting ¹	Birds present at a location during period(s) of darkness.
Loafing ²	Birds observed resting, usually in trees, while not engaged in any
	other listed behaviors.
Flyover ²	Entire flock flying in a directional manner, without landing. Short
	flight movements by one or a few birds while the flock was engaged
	in one of the other listed behaviors were not considered flyovers.

Table 1. Description of Pinyon Jay behavior types that were recorded duringobservational and radio-telemetry surveys whenever possible.

¹Due to small sample size, this behavior type was used only for ordination analyses.

²Observations for these behavior types were excluded from analysis.

203

Radio-telemetry surveys were also used to obtain Pinyon Jay locations for some of the studied flocks. Two methods were used to capture Pinyon Jays for radio-tagging; baited walk-in traps and mist nets. Traps were used where Pinyon Jays could be consistently drawn (determined by game cameras) to a supplemental food station baited with shelled peanuts, sunflower seeds, and dried corn. In these areas, a home-made wood and mesh walk-in trap (0.6 x 1.2x 0.9 m) with an

209 open door was placed at the site, and bait spread periodically inside the trap to habituate birds to 210 entering the trap. When habituation was sufficient (determined by camera traps), capture attempts were made by rigging the door for remote manual release, observing activity at the trap 211 from a blind ~ 25 m from the trap, and releasing the door with a pull cord when Pinyon Jays 212 were inside the trap. Mist-nets were used in areas where walk-in traps were not viable, specially 213 214 in locations routinely visited by Pinyon Jays where nets could be deployed without being easily detected by birds. Mist nets (60 mm mesh) were arrayed either singly, as doubles, or stacked, 215 depending on the geometry of the woodland opening where they were erected. In some cases, 216 217 call playback was also used to try to draw birds into the nets. Any Pinyon Jays captured by walkin trap or mist net were weighed and aged; standard aluminum leg bands (U.S. Geological 218 219 Survey) were attached; and radio transmitters (Advanced Telemetry Systems model A2450) 220 were glued onto feather stubble clipped to ~ 0.3 cm above skin level in the interscapular area. No more than six individuals from any single flock were radio-tagged, since data were collected to 221 characterize flocks rather than individual birds. Captured birds were handled and processed only 222 by experienced individuals holding a U.S. Fish and Wildlife Service master banding permit. 223 Radio-tagged birds were manually tracked using a handheld three-element Yagi antenna with an 224 225 Advanced Telemetry Systems R410 or R100 receiver. The goal of radio-telemetry surveys was to collect hourly locations over one entire daylight cycle per week for each flock, either in a 226 single long session or over several sessions of 3-5 hours on different days and at different 227 228 times. Most often, telemetry fixes from one or more radio-tagged flock members were used to approach the flock and establish visual contact, at which point locational and behavior type 229 230 attributes were collected exactly as described above for observational surveys. Occasionally, 231 flock locations were estimated by biangulation or triangulation of telemetry bearings that were

post-processed using LOAS software (Ecological Software Solutions, LLC). In cases where the 232 flock was not directly observed, behavior type was only recorded when it could be reasonably 233 234 inferred based on previous observations (i.e. return to a nest colony location) or context (roosting locations at after sunset). 235 236 For a given flock, locations could be obtained by either observational surveys, radio-telemetry 237 surveys, or both, but because both approaches ultimately relied on the same observational 238 process, we regarded the resulting data as comparable. Initially, radio-telemetry was the 239 240 preferred survey approach, but by later data collection periods we determined that visual contact with most flocks could routinely be established without reliance on radio-tagged flock members, 241 and our efforts to capture birds for radio-telemetry were discontinued. 242 243 The full set of Pinyon Jay locations recorded during field work were filtered and processed prior 244 to analysis. First, any locations where no behavior type was recorded were deleted. Next, all 245 "flyover" locations and loafing locations (Table 1) were deleted, based on the premise that these 246 could occur throughout and sometimes beyond the flock's core home range. Finally, locations 247 248 that represented the same flock engaged in the same behavior at the same location were combined as follows: 249 250 1) All nesting locations for a single flock were spatially averaged using the Mean Center 251 tool in ArcMap 10.5 (ESRI, Redlands CA), based on the premise that at a given time, a flock has only one nesting area. 252 2) If caching, foraging, or roosting locations were closer together than 71.8 m, they were 253 254 spatially averaged to generate a single location, as above. This was the smallest threshold

255	distance sufficient to prevent any overlap between the 0.405-ha habitat plots used to
256	assess habitat (see below), so this process smoothed Pinyon Jay locations to a spatial
257	scale that matched the habitat assessment scale.
258	
259	After these steps, 152 Pinyon Jay locations with recorded behaviors were retained for analysis
260	(see Table S1).
261	
262	Data collection procedures described in this section were primarily observational and were not
263	submitted to or approved by an Institutional Animal Care and Use Committee. Field work that
264	involved capture, radio-tagging, and release of Pinyon Jays was conducted under U.S.
265	Department of the Interior Federal Bird Banding Permit # 22912, Idaho Fish and Game
266	Department Collection Permit # 120724, and Nevada Department of Wildlife Collecting Permit
267	# 29948.
268	
269	Control site selection (level 2 heading)
270	
271	Control sites were selected from the pre-existing FIA data set of plots visited and measured
272	between 2005-2013. FIA data provide a probabilistic and geographically unbiased assessment of
273	forest / woodland attributes over time and space [46, 47] and a robust dataset to describe habitat
274	for multiple species [48-52]. One FIA plot is randomly positioned within every cell of a
275	sampling grid that covers all public and private forest land in the United States, with an overall
276	density of one plot per 2,428 ha (6,000 acres) within the extent of that sampling frame [53]. Each
277	year, 10% of these plots are surveyed or re-surveyed in the western U.S. using a spatially-

278	interpenetrating sampling design that avoids conflation of spatial with temporal trends [46]. The	
279	criteria used to select the subset of FIA plots that were appropriate control sites for this study	
280	were as follows:	
281		
282	1) The FIA plot had to be < 200 km from the nearest Pinyon Jay location retained for	
283	analysis.	
284	2) Presence of pinyon-juniper woodland within the FIA plot had to be confirmed by direct	
285	observation of the field assessment crew during the most recent assessment visit. A	
286	woodland type classification based solely on remote-sensing data was not sufficient to	
287	meet this criterion.	
288	3) The site had to be located in both the Central Great Basin Ecoregion [43] and in BCR 9.	
289	4) The most recent assessment visit had to have occurred in 2005 or later.	
290		
291	In total, 346 FIA plots from the larger data set met these criteria (Fig 3) and were included in our	
292	analysis (see Table S1). Each control site was assigned a regional attribute that corresponded to	
293	the closest Pinyon Jay study area ($n = 212$ for the Eastern Nevada region, $n = 81$ for the Southern	
294	Idaho region, and $n = 53$ for the Central Nevada region). Control sites were not distributed	
295	symmetrically around the Pinyon Jay study areas (especially for Southern Idaho) because their	
296	extent was constrained by the distribution of pinyon-juniper woodland and by the USFS site	
297	selection process.	
298		
299	Habitat assessment (level 2 heading)	

305	performed by USFS crews fully trained in FIA protocols and procedures. Control sites were
306	assessed as part of routine USFS operations in various years between 2005-2013 [56-58].
307	
308	FIA plot layout is based on a 0.405 ha circle that defines four subplots of 7.3 m diameter within
309	which actual measurements are made. One subplot is located at the center of the larger circle,
310	and the other three subplots have their centers equally spaced along its circumference (Fig 4). On
311	a standard forested FIA plot, over 120 attributes are measured within each subplot to characterize
312	location, condition, and vegetation [59]. Subplot data are then averaged or summed over subplots
313	as appropriate and extrapolated to generate data at the whole-plot scale. The subset of FIA
314	attributes that were considered for use in this analysis are presented and briefly described in
315	Table 2.
316	
317	Fig 4. Schematic diagram of a USFS FIA plot layout. Data used in this study consisted of
318	full-plot values produced by either summing or averaging sub-plot data.

319

Table 2. Attributes describing Pinyon Jay habitat that were considered in this study. Brief descriptions of attributes are provided parenthetically, with complete descriptions of associated methodologies available in [59]. The 2^{nd} , 3^{rd} , and 4^{th} columns indicate whether or not an attribute was used (Y = yes, N = No, NA = categorical attribute, not applicable) for the ordinations, logistic regressions, and data visualizations presented below. Footnotes provide additional explanations about attribute use considerations.

Attribute	Ordination	Logistic Regression	Data Visualization
FIA Attributes			l
Elevation (measured in feet at plot center)	Y	Y	Y
Slope (expressed as slope percentage, or {{rise/run} x 100} at plot center)	Y	Y	Y
Habitat Type [60]	NA	N ¹	N
Stand Age (age in years of the oldest pinyon pine or juniper tree on plot, as determined by coring)	Y	Y	Y
Stand Density Index (index of three- dimensional tree density within stand [60])	N ²	N ²	Y ²
Canopy Cover (% by ocular estimation)	Y	N ³	N
Tree Cover (% by ocular estimation)	Y	Y	Y
Shrub Cover (% by ocular estimation)	Y	Y	Y
Forb Cover (% by ocular estimation)	Y	Y	Y
Grass Cover (% by ocular estimation)	Y	Y	Y
Woody Debris (count of pieces of woody debris material along transects for seven different size diameter classes, defined by twig / branch diameter ranges)	Y	Y ⁴	Y ⁴
Distance to Road (km from plot center, assigned using topographic maps; original ordinal ranges converted to range midpoints)	Y	Y	Y
Disturbance Presence ("yes-no", for any disturbances within the last five years)	NA	Y	N
Disturbance Type (categories of silvicultural treatment or other disturbance occurring within the previous five years)	NA	N ⁵	N
Non-FIA Attribute			
Distance to Edge (Distance to the lower- elevation woodland-shrubland ecotone, measured directly in on imagery in ArcMap 10.5)	N ⁶	N ⁶	Y

¹ All sites used in analysis were characterized by presence of at least some pinon pine and/or juniper trees, but the FIA habitat type distinctions were too fine-grained (33 different types, median number of sites / type = 5) for inclusion in analysis.

²Omitted from analyses due to high correlations with other attributes, but included in data visualizations because of possible synthetic interpretational value.

³Omitted because of high correlation to Tree Cover attribute (r = 0.68).

⁴Reduced to a single attribute by Principle Component Analysis that described 86.1% of variation across all original classes.

⁵The level of articulation was too fine for the limited number (n=68) of disturbed sites and too unevenly distributed among types, so only the "yes-no" disturbance attribute was retained.

320

321	Based on our field observations of Pinyon Jay landscape use over the course of the study, we
322	decide to create one additional non-FIA attribute, "Distance to Edge" (Table 2) which is the
323	shortest linear distance between a Pinyon Jay location or control site and the lower-elevation
324	woodland-shrubland ecotone. First, polylines were digitized in ArcMap 10.5 to delineate the
325	approximate ecotonal boundary based on visual examination of imagery. This process did not
326	delineate woodland – shrubland boundaries inside well-defined woodland patches, but instead
327	defined distinct woodland patches based on their lowest-elevation ecotonal boundary. Then, the
328	shortest distance from each Pinyon Jay location or control site to the polyline was computed
329	using the Near tool in ArcMap 10.5. This value was usually positive, but could be negative if a
330	Pinyon Jay location was in shrubland at a lower elevation than the polyline. Because the
331	Distance to Edge metric was not a FIA attribute, it was used only for data visualizations, not for
332	statistical analysis.

333

334 Analysis (level 2 heading)

⁶Omitted from ordinations and logistic regression because attribute estimation process was not part of the standardized FIA protocol. Retained in data visualizations for possible interpretive value

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336 *Data* (level 3 heading)

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338 The complete data set used for all analyses and summarizations is provided in Table S1.

339

340 *Ordination* (level 3 heading)

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To visualize how the habitat characteristics of Pinyon Jay locations for each behavior type 342 343 overlapped with control sites, we performed region-specific ordinations on continuous FIA habitat attributes (Table 2) using nonmetric multidimensional scaling (NMDS). NMDS 344 optimizes the non-parametric monotonic relationship among the data and the visualization space, 345 providing the best low-dimensional representation [61-63]. All ordinated attributes were 346 standardized with a z-transformation across all of the regions prior to the NMDS to promote 347 optimization, which was defined as minimizing the stress value [63]. The NMDS was performed 348 with the metaMDS function in the vegan package (v 2.5-5; [64]) in R (v3.5.1; [65]), using the 349 Euclidian distance with two dimensions to force a visualizable representation. The maximum 350 number of iterations was increased from the default of 200 to 10¹⁰ and the maximum number of 351 runs was increased from 20 to 1,000 to achieve convergent solutions across repeated runs. 352 Defaults for auto-transformation, extended dissimilarities, and weighted average scoring were 353 354 turned off because they were not applicable to our transformed input data set. 355

356 *Logistic Regression* (level 3 heading)

358 To evaluate the effects of measured habitat attributes on Pinyon Jay occupancy by behavior type [42, 44, 66] we used logistic regressions for each behavior type that had sufficient data (i.e. 359 caching, foraging, nesting). Roosting location were not analyzed because of low sample size 360 (n=3). Because the ratio of Pinyon Jay locations to control sites was low, the odds ratio output 361 from logistic regression can be treated as an approximation to the resource selection function 362 363 [42, 67, 68]. However, it is important to recognize that the intercept value of the logistic regression does not estimate the overall use probability, as the Pinyon Jay locations were not 364 365 randomly selected [42]. 366 Initial evaluation of available predictor attributes (Table 2) consisted of plotting data pairs, 367 evaluating correlations, and preliminary overall model fitting to ensure base-level convergence. 368 369 Several attributes were eliminated from the analysis due to high correlations with other attributes or highly uneven distribution of values. Others were combined into a single attribute with 370 principle components analysis (Table 2). All continuous attributes used for analysis (Table 2) 371 were converted to metric units and z-transformed to facilitate model fitting and term comparison. 372 373 374 For the logistic regression models, we split the control sites assigned to each region (see above) according to behavior types in proportion to behavior frequency, rather than "reusing" control 375 sites across multiple behavior types. Splitting was randomized and permutated 10,000 times to 376 377 account for variation in the dataset splitting process. For each permutation, the control data were first split among the behaviors types within each region, then the data for a given behavior type 378 were combined across the three regions and analyzed using a generalized (binomial) mixed 379 380 model fit with the glmer function in the lme4 package (v1.1-19; [69]) in R (v3.5.1; [65]). The

permutations were then combined to integrate over the sample allocation variation and estimate 381 overall terms. This was done by first discarding any permutations that did not converge due to 382 unreasonable splits of control sites that could occur within the randomization. Then, for each 383 permutation, a single set of fixed effects parameters were drawn from the multivariate normal 384 distribution described by the glmer model fit using the rmvnorm function in the mvtnorm 385 386 package (v1.0-8; [70]) in R (v3.5.1; [65]). By drawing from the distribution within each permutation, the full set of parameter values across permutations includes both parameter 387 estimation uncertainty and data allocation uncertainty. To avoid distributional assumptions in 388 389 evaluating the significance of the parameter estimates, we tested whether the estimate significantly differed from 0 by using a permutation-style two-tailed approach [71]. This 390 involved using the empirical cumulative distribution function (calculated using the ecdf function 391 392 in the stats package in base R (v3.5.1; [65]) to estimate the two tail probabilities with respect to 0, taking the smaller value as the focal tail, and doubling that tail's probability. We combined the 393 estimates of the random effects (one for each successful permutation) across all of the 394 permutations to generate the distribution of values for each random effects term across the 395 uncertainty in control data allocation. 396

397

Within-sample classification accuracy of logistic regression models for each Pinyon Jay behavior
type was averaged over all 10,000 permutations. Because the number of Pinyon Jay locations for
each behavior type was limited, we did not withhold a subset of locations for external validation.

402 *Data visualization* (level 3 heading)

403

404	To aid in the interpreting statistical results and to highlight univariate patterns of interest, box
405	plots were created for each continuous habitat attribute shown in Table 2, contrasting the
406	distribution of attribute values for behavior-specific Pinyon Jay locations and control points.
407	
408	Results (level 1 heading)
409	
410	Data summary (level 2 heading)
411	
412	Behavior-specific Pinyon Jay locations ($n = 152$) were obtained from 15 different flocks. Details
413	about distribution of Pinyon Jay behavior type locations among study regions, apportionment of
414	control sites, number of flocks per study area, and methods of data collection used within study
415	areas are summarized in Table 3. Pinyon Jay data were not fully symmetrical among the study
416	areas. Nesting was not recorded in Southern Idaho because the data collection period excluded
417	the breeding season, and our data recording protocol in 2008-2009 for Eastern Nevada did not
418	specify the foraging behavior type. Only caching locations were recorded in all three study areas
419	and only in the Central Nevada study area were all three major behavior types (caching,
420	foraging, and nesting) recorded.

421

Table 3. Summary of Pinyon Jay locations after data processing, by behavior type and by region / study area. Shown parenthetically in $2^{nd} - 5^{th}$ columns are the number of control sites assigned to each unique combination of study region x behavior type within logistic regression models as described in above. The final column summarizes the number of different Pinyon Jay flocks from which data were collected in each study area, with the data collection methods used shown in brackets (T = telemetry surveys, with number of deployed radio tags in parentheses: O = observational surveys).

Study Region /	# Caching	# Foraging	# Nesting	# Roosting	# Flocks [Method of
Area	Sites	Sites	Sites	Sites	Study]

Eastern Nevada	12 (106)	0 (0)	12 (106)	3 (N/A)	2 flocks [Flock #1 = T(6); Flock #2 = T(6)]
Southern Idaho	32 (51)	19 (30)	0 (0)	0 (N/A)	2 flocks [Flock #1 = O & T(6); Flock #2 = O & T(2)]
Central Nevada	26 (18)	22 (15)	28 (20)	0 (N/A)	11 flocks [All = O]

422

423

424 **Ordination** (level 2 heading)

425

The NMDS ordination found convergent solutions within 28, 388, and 20 runs for the Eastern 426 Nevada, Southern Idaho, and Central Nevada regions, respectively (Fig 5). Each of the 427 428 ordinations was well-correlated with true distances with stress values of 0.183, 0.127, and 0.161, respectively. Notably, for all three regions, Pinyon Jay locations formed distinct clusters in the 429 430 NMDS plots that were easily distinguishable from the broader distribution of control sites (Fig 5) 431 Degree of overlap among Pinyon Jay behavior type clusters varied somewhat across study regions, though nesting locations and caching locations were distinct in the two regions where 432 433 both types of data were available. NMDS results suggested that the locations where Pinyon Jays occurred in the three study areas tended to be different than typical control sites within the 434 corresponding study regions, and that Pinyon Jays tended to use different habitats for different 435 behaviors. 436

437

Fig 5. NMDS ordination results for each region, by location type. Note that each region's
ordination is independent and the axes cannot be compared among them.

440

441 **Logistic regression** (level 2 heading)

442

Logistic regression models offer potential insights into which habitat covariates underpin the 443 differentiation seen in the ordinations. We note, however, that within our logistic regressions, 444 many predictors that had strong and statistically significant effects for a majority of iterations in 445 the control site allocation process became non-significant when all iterations were combined. 446 447 Because of this sensitivity to control site allocation, examination of data visualizations (next section) may assist in the interpretation of model results. Internal classification accuracy of 448 behavior-specific Pinyon Jay locations versus control sites (averaged overall all iterations) was 449 450 high (0.890 for the caching model, 0.863 for the foraging model, and 0.920 for the nesting model). 451

452

453 Models indicated that Pinyon Jay caching locations were more likely to occur with lower slope, lower tree cover, increased woody debris, shorter distance to roads, and more disturbance than 454 control sites (Table 4). There was also a strong effect of decreased elevation, though it was not 455 significant when averaged across all control allocation iterations. None of the predictors for 456 Pinyon Jay foraging locations were statistically significant when averaged across all iterations 457 458 due to high standard errors, but the largest effect sizes were noted for lower slope, less grass and forb cover, increased woody debris, and shorter distance to roads compared with control sites 459 (Table 4). Pinyon Jay nesting locations were more likely to occur at lower elevations with 460 461 decreased forb cover and increased woody debris compared to control sites (Table 4). Across all three Pinyon Jay behavior types, occupancy probability generally increased with lower elevation, 462 lower slope, lower forb cover, shorter distance to roads, and increased woody debris compared to 463

- 464 control sites (Table 4). Lower tree cover was a marginally significant predictor for caching
- 465 locations but was not a significant predictor for foraging and nesting locations.

466

Table 4. Logistic regression results over all control site allocation iterations for the caching, foraging, and nesting location analyses. Fixed effects are reported as mean and standard error of the estimate and the two-tailed p value; random effects are reported as mean and standard error of the estimate and the probability (fraction of permutations) that the term was equal to 0. Bolded terms are significant at $\alpha = 0.05$.

C	ACHING LOCA	TIONS	
	Mean	Standard Error	р
Fixed Effect			
Intercept	-3.687	1.162	0.001
Elevation	-0.405	0.585	0.481
Slope	-2.066	0.557	< 0.0001
Stand Age	-0.177	0.432	0.654
Tree Cover	-0.913	0.553	0.075
Shrub Cover	0.251	0.349	0.445
Forb Cover	-0.021	0.3	0.904
Grass Cover	0.377	0.439	0.385
Woody Debris	1.235	0.818	0.010
Distance to Road	-2.712	0.789	< 0.0001
Disturbance	1.971	0.951	0.022
Random Effect			
Eastern Nevada: Intercept	1.838	0.413	0.0001
Southern Idaho: Intercept	-1.320	0.301	0.0001
Central Nevada: Intercept	-0.522	0.288	0.0001
FC	DRAGING LOCA	TIONS	
Fixed Effect			
Intercept	-5.486	7.418	0.044
Elevation	-1.566	2.790	0.317
Slope	-4.184	6.299	0.058
Stand Age	-2.013	3.641	0.236
Tree Cover	1.931	3.079	0.200
Shrub Cover	1.380	2.479	0.311
Forb Cover	-9.236	14.819	0.080
Grass Cover	-4.970	8.384	0.113
Wood Debris	4.419	9.650	0.053
Distance to Road	-3.326	4.848	0.063
Disturbance	-1.700	75.272	0.555
Random Effect		·	·

0.686	1.076	0.290			
N/A	N/A	N/A			
-0.707	1.327	0.290			
Central Nevada: Intercept -0.707 1.327 0.290 NESTING LOCATIONS					
-4.723	2.623	0.021			
-2.445	1.600	0.004			
-1.249	1.090	0.154			
0.528	1.016	0.564			
0.500	1.030	0.570			
0.261	0.848	0.743			
-7.110	4.247	0.022			
0.123	1.256	0.983			
2.156	1.266	0.003			
-1.118	1.291	0.289			
2.606	2.406	0.115			
2.116	0.903	0			
-2.088	0.904	0			
NA	NA	NA			
	N/A -0.707 ESTING LOCAT -4.723 -2.445 -1.249 0.528 0.500 0.261 -7.110 0.123 2.156 -1.118 2.606 2.116 -2.088	N/A N/A -0.707 1.327 ESTING LOCATIONS -4.723 2.623 -2.445 1.600 -1.249 1.090 0.528 1.016 0.500 1.030 0.261 0.848 -7.110 4.247 0.123 1.256 2.156 1.266 -1.118 1.291 2.606 2.406 2.116 0.903 -2.088 0.904			

The random effects components of the three models were all estimated to be non-zero, although
the foraging model estimated a zero-value in 29% of allocation iterations, whereas the caching
model estimated a zero-value in < 1% of iterations. The additional complexity introduced by a
singularity/boundary condition (a zero-value random effect) within many foraging model
iterations may have contributed to the variability (and thus reduced significance) seen in the
parameter estimates. **Data visualizations** (level 2 heading)

478	Fig 6 shows box plots for all FIA attributes included in logistic regression models combined
479	across all study regions, and Fig 7 shows box plots for two additional habitat attributes (the FIA
480	Stand Density Index attribute and the non-FIA Distance to Edge attribute) that were not included
481	in logistic regressions, but which showed patterns of interest with regard to Pinyon Jay
482	occupancy. Notable patterns in these box plots are as follows:
483	
484	1) Across all study regions, locations used by Pinyon Jays appeared to be a distinct subset
485	available woodland habitat with regard to many habitat attributes. This is consistent with
486	the patterns observed in the NMDS ordination (Fig 5). Additionally, locations used by
487	Pinyon Jays for different behaviors appeared to vary with regard to multiple habitat
488	attributes.
489	2) Compared to available habitat, caching locations were concentrated in lower elevation,
490	lower-slope areas with young woodland stands, low tree cover, and high shrub, forb, and
491	grass cover. The Stand Density Index was typically very low for caching locations, which
492	were also highly concentrated near the woodland-shrubland ecotone (i.e. low Distance to
493	Edge values). In fact, many caching locations occurred in the pure shrubland habitat
494	located down-slope from the woodland-shrubland ecotone (note that these pure
495	shrublands were not represented in the sample of FIA control sites).
496	3) Foraging locations were also concentrated in lower elevation and lower slope areas, but
497	were somewhat higher and steeper than caching locations, with somewhat higher stand
498	densities. Foraging locations had more woody debris than typical control sites, but stand
499	age, tree cover, forb cover, and grass cover were comparable to control sites. Shrub cover
500	in foraging locations was highly variable, but tended to be higher than in control sites.

501		Foraging locations were close to the woodland-shrubland ecotone, with lower stand
502		density indices, though to a less extent than caching locations
503	4)	Nesting locations also tended to occur at lower elevations and lower slopes, but to a
504		lesser degree than foraging and caching locations. Stand age and shrub cover were
505		comparable between nesting locations and control sites, but nesting locations had higher
506		tree cover, lower forb cover, and more woody debris. Stand density was somewhat lower
507		for nesting locations than for control sites, but with considerable overlap. Nesting
508		locations were also concentrated close to the woodland-shrubland ecotone, but to a lesser
509		degree than foraging locations.
510	5)	There was a distinct pattern of increasing elevation and slope, increasing distance from
511		edge, and increasing stand density moving from caching locations to foraging locations to
512		nesting locations, but all three behavior types had lower values for these attributes than
513		typical control sites.
514		
515		Fig 6: Box plots for all continuous attributes used in logistic regression models, as
515 516		Fig 6: Box plots for all continuous attributes used in logistic regression models, as described in Table 2. Y-axis codes are Co = control sites, N = Pinyon Jay nesting
516		described in Table 2. Y-axis codes are Co = control sites, N = Pinyon Jay nesting
516 517		described in Table 2. Y-axis codes are Co = control sites, N = Pinyon Jay nesting locations, F = Pinyon Jay foraging locations, and Ca = Pinyon Jay caching locations.
516 517 518		described in Table 2. Y-axis codes are Co = control sites, N = Pinyon Jay nesting locations, F = Pinyon Jay foraging locations, and Ca = Pinyon Jay caching locations. For better visual clarity, the extreme high range of observed Forb Cover values (15
516 517 518 519		described in Table 2. Y-axis codes are Co = control sites, N = Pinyon Jay nesting locations, F = Pinyon Jay foraging locations, and Ca = Pinyon Jay caching locations. For better visual clarity, the extreme high range of observed Forb Cover values (15
516 517 518 519 520		 described in Table 2. Y-axis codes are Co = control sites, N = Pinyon Jay nesting locations, F = Pinyon Jay foraging locations, and Ca = Pinyon Jay caching locations. For better visual clarity, the extreme high range of observed Forb Cover values (15 – 25%) is truncated, omitting a small number of Co sites and Ca locations.
516 517 518 519 520 521		 described in Table 2. Y-axis codes are Co = control sites, N = Pinyon Jay nesting locations, F = Pinyon Jay foraging locations, and Ca = Pinyon Jay caching locations. For better visual clarity, the extreme high range of observed Forb Cover values (15 – 25%) is truncated, omitting a small number of Co sites and Ca locations. Fig 7: Box plots for two habitat attributes not used in logistic regression models, as

524	For better visual clarity, the extreme high range of observed Distance to Edge values
525	(6,000 – 12,000 m) values are truncated, omitting a small number of Co sites.
526	
527	
528	Discussion (level 1 heading)
529	
530	Main findings and significance (level 2 heading)
531	
532	This study offers the first systematic description of Pinyon Jay occupancy patterns and behavior-
533	specific habitat characteristics in the Great Basin. The combination of ordinations, logistic
534	regressions, and data visualizations presented in this study suggest that Pinyon Jays use pinyon-
535	juniper woodlands selectively. All Pinyon Jay locations in our study areas were concentrated in
536	or near lower-elevation, flatter woodlands and were less common in higher-elevation, steeper
537	woodlands. Additionally, the areas used for different Pinyon Jay behaviors appear to have
538	distinctive (but overlapping) habitat profiles, with caching, foraging, and nesting arrayed
539	sequentially along gradients of increasing slope, elevation, and stand density. Similar patterns of
540	Pinyon Jay caching and nesting activities partitioned along elevation and stocking gradients were
541	observed by Johnson et al. [23] within a pinyon-juniper (P. edulis / Juniperus spp. association)
542	woodland system in New Mexico, suggesting that habitat partitioning by behavior along an
543	elevational gradient could be present across a broader physiographic range than our study
544	regions.
545	

Pinyon Jay caching locations were concentrated in open woodland stands with high shrub and 546 grass cover, which are similar to the Phase I (early successional) pinyon-juniper woodlands 547 defined in the classification scheme by Miller et al. [33], and sometimes occurred in pure 548 shrublands. This occurrence pattern could have a mutualistic explanation [3]. From the pinyon 549 pine perspective, seedlings likely experience less competition from established trees in more 550 551 open areas, and seeds placed next to shrubs, rocks, or woody debris in otherwise open areas may benefit from favorable microsite conditions created and maintained by those features [72, 73]. 552 From the Pinyon Jay perspective, pinyon pine seeds cached away from their source of origin may 553 554 be less likely to be discovered and eaten by small mammals that specialize on pinyon seeds [73, 74]. 555

556

557 Pinyon Jay foraging locations generally occurred in older (though still relatively young) stands than caching locations, across a wide range of tree cover values. Given that foraging behavior as 558 defined in our study encompassed the gathering of diverse food items from trees, shrubs, and 559 ground, areas with these characteristics may offer a beneficial combination of pinyon pines in 560 their most productive seed-bearing years [75, 76] interspersed with areas where abundant insect 561 prey is available due to higher shrub or ground cover [77]. The habitat characteristics of Pinyon 562 Jay foraging locations correspond to a mosaic of Phase I and Phase II pinyon-juniper 563 564 successional stages [33].

565

Pinyon Jay nesting locations tended to be concentrated in areas with higher tree cover and more
woody debris, presumably because of the concealment they offer [23, 78]. However, like caching
and foraging locations, nesting locations were concentrated in lower elevation, lower slope areas,

569 and steeper, higher sites that otherwise offered good concealment for nesting locations appeared to be avoided. Pinyon Jay nesting locations correspond best with the denser portion of the Phase 570 571 II class of pinyon-juniper woodlands, but may also include some Phase III areas [33]. 572 All Pinyon Jay locations, regardless of behavior type, were concentrated in lower-elevation 573 574 woodlands (most likely a mix of Phase I and Phase II classes) near the woodland-shrubland ecotone. This could occur because of the longer snow-free season of lower elevations, or the 575 presence of a mosaic of desirable habitat characteristics needed to support different behavior 576 577 types. Phase I and Phase II woodlands are relatively common at lower elevations where Pinyon Jay locations are concentrated, whereas the proportion of Phase III woodlands tends to increase 578 579 with increasing elevations based on our field observations.

580

In addition to providing important information about Pinyon Jay occupancy patterns and habitat 581 582 use, these findings are potentially significant for vegetation management planning and implementation because Pinyon Jays in our three study areas appear to prefer the same lower-583 elevation, relatively-open woodlands where most woodland removal management is performed 584 585 [79, 80]. These vegetation management projects, which are most often conducted to create or improve habitat for Greater Sage-Grouse [81] (but see Miller et al. [22] and Somershoe et al. 586 587 [15] for others reasons for woodland treatments), have resulted in the removal of an estimated 588 45,000 ha of pinyon-juniper woodland in the Great Basin portions of Nevada, Utah, and Idaho over the last eight years alone (Witt, unpublished USFS data). The pace of this activity appears 589 to be steady or accelerating, and may therefore be or become a significant factor affecting Pinyon 590 591 Jay populations, either negatively or positively. Information from other regions suggests that

592	woodla	and treatments can have unintended effects on Pinyon Jays. For example, Johnson et al.				
593	[82] fo	und that a fuels treatment within pinyon-juniper woodlands in northern New Mexico that				
594	reduced tree density by almost 90 percent prompted the local Pinyon Jay flock to avoid the					
595	treated area altogether. To date, however, almost no direct monitoring has been conducted in the					
596	Great l	Basin to determine if and how Pinyon Jay flocks respond to vegetation management				
597	project	is that occur within or close to their home ranges.				
598						
599	Inter	pretational considerations (level 2 heading)				
600						
601	The fir	ndings presented in this study should be interpreted with the following considerations in				
602	mind:					
603	1)	Pinyon Jay data were collected at the three distinct study areas that collectively				
604		encompassed 175,630 ha. Although this was a large area, it represents only a small				
605		portion of the Great Basin region that we would like to characterize.				
606	2)	This study combined data from three distinct projects that covered different years and				
607		seasons. This is most immediately relevant to interpreting the foraging model, given that				
608		seasonal variation in foraging behaviors and locations are plausible.				
609	3)	We equated "potential habitat" for Pinyon Jays to all pinyon-juniper woodlands lying				
610		within 200 km of any Pinyon Jay study area, as sampled by FIA plots. Although				
611		inferences from this study can cautiously be extended to the pinyon-juniper woodlands				
612		beyond our immediate Pinyon Jay study areas (subject to confirmation in future studies;				
613		see Johnson and Sadoti [78] for caveats about model transferability to similar systems) it				
614		does not extend to other forest types or regions where Pinyon Jays occur.				

615 4) Our analysis does not distinguish between flocks within a study area, and does not allow
616 us to draw inferences about inter-flock variability with regard to behavior-specific
617 occupancy patterns.

5) The iterative allocation of control sites among Pinyon Jay behavior types in logistic
regression modeling was necessary, but it could have diluted the statistical significance of
some important predictors of occupancy. Future modeling efforts where the spatial
extents and sample sizes of Pinyon Jay data and control data are better matched should
reduce this issue. Models created from data sets with a large sample of Pinyon Jay
locations will also allow data to be withheld from the model building process and used
for external validation.

6) Interpreting the relationship between Pinyon Jay occurrence and distance to road is
complex and potentially non-causal. Roads density is typically higher in lower-elevation,
flatter areas, and Pinyon Jays prefer these areas for reasons completely unrelated to the
proximity of roads. However, one author has suggested the vegetation typically present
alongside graded, unpaved roads may provide valuable foraging opportunities for Pinyon
Jays [83].

7) The Distance to Edge attribute used for data visualizations shows clear contrasts across
behavior-specific Pinyon Jay locations and control sites, but it needs to be further
investigated using more formal methods for delineating ecotones. Additionally, the
patterns seen in our data (Fig 7) were enhanced because control sites by definition
excluded the pure or near-pure shrublands that comprised a significant proportion of
Pinyon Jay caching locations, and a smaller proportion of foraging locations.

637

Currently, we are analyzing a separate Pinyon Jay data set derived from a long-term statewide
bird monitoring program in Nevada. Because these data were obtained from a broader-scale
fully-randomized sampling design and used a fully standardized survey protocol, they should
provide a useful independent characterization of Pinyon Jay occupancy patterns in the Great
Basin.

643

644 **Conclusions and recommendations** (level 2 heading)

645

Pinyon Jay populations have been declining precipitously for at least the last half-century, while 646 647 the pinyon-juniper woodlands that they inhabit in the Great Basin are thought by many to have 648 been expanding at unprecedented rates [84-87]. Given this apparent paradox, identifying the reasons for Pinyon Jay declines is critical for defining constructive conservation actions that 649 ensure the species' long-term viability [3, 15]. This urgency is amplified by the widespread and 650 651 potentially accelerating woodland management activities in the Great Basin that prioritize creation or preservation of shrublands without a clear understanding of their impacts on Pinyon 652 653 Jays and other woodland-associated birds. Progress towards a more inclusive management paradigm can be achieved through: a) better knowledge of Pinyon Jay ecology and habitat 654 requirements, b) monitoring of management impacts, c) better understanding of the ecology and 655 dynamics of the woodlands that comprise Pinyon Jay habitat, and d) integration of knowledge 656 obtained from these three areas into existing vegetation management protocols and guidance. 657 658

A fundamental need is for more robust, spatially-extensive data characterizing Pinyon Jay
occupancy patterns and habitat use as a function of region, season, and behavior type, both

661 across and within the individual flock level. To maximize their value, these data would ideally be gathered using a standardized survey protocol. Pinyon Jays, however, present multiple 662 challenges to the field biologist, study designer, and data analyst [15], and approaches suitable 663 for typical passerine birds may be suboptimal for Pinyon Jays for several reasons. Unlike species 664 where a single breeding pair occupies a clearly-delineated territory at all times during the 665 666 breeding season, Pinyon Jays occupy (and presumably select) habitat at the flock and subflock level. Pinyon Jays are also year-round residents, and protecting breeding habitat alone may be 667 insufficient for effective conservation. The Pinyon Jay's pattern of habitat use, which involves 668 669 temporal flock movements across a relatively large home range to accommodate different behaviors and take advantage of seasonally-varying food resources, has potentially profound 670 effects on both the detection properties of a given survey protocol and the ecologically-legitimate 671 672 interpretation of those detection patterns. As a simple example, a Pinyon Jay flock may be frequently absent from a critically-important subset of its home range, either during portions of 673 the day, or during entire seasons. Similarly, roaming flocks may frequently fly over or loaf in 674 areas of the home range that are not critical to home range quality or viability. To provide 675 accurate and actionable information about the habitat requirements of Pinyon Jays, survey 676 677 protocols and research study designs need to account for these realities appropriately, operate at 678 scales that reflect actual Pinyon Jay habitat selection patterns, and be guided by a sampling 679 framework that produces well-balanced data suitable for presence / absence modeling. The 680 multi-agency Pinyon Jay Working Group [15] is currently actively investigating options for standardized Pinyon Jay survey protocols. The same group's Pinyon Jay Conservation Strategy 681 [15] also noted that some of the information needed to better characterize Pinyon Jay habitat 682 683 requirements could be obtained by systematically monitoring Pinyon Jay responses to vegetation

management activities, especially in situations where their pre-treatment presence has beenconfirmed by baseline or clearance surveys.

686

With regard to pinyon-juniper woodlands, their structural attributes and other characteristics that 687 might be limiting to Pinyon Jay populations need to be further studied. We suggest that it may be 688 689 especially important to identify the correlates or profiles of tree stands and landscapes that exhibit a predictable and/or abundant pinyon pine mast [22]. Our preliminary review of FIA data 690 collected in Nevada between 2006-2015 suggests that woodlands matching the structural 691 692 characteristics Pinyon Jays used for foraging in this study are 5-7 times less extensive than nesting or caching habitat in Nevada (unpublished USFS data). Presence of reliably productive 693 694 stands within the home range could be especially important to Pinyon Jays during years of more 695 generally depressed pine mast production. Given evidence of reduced mast production in pinyon pine [88], and associated changes in habitat use by Pinyon Jays [24] in some areas affected by 696 climate change, it might be critical to long-term Pinyon Jay conservation to systematically 697 investigate the quality and quantity of good foraging areas. 698

699

In addition, more research is needed to better clarify the degree to which woodland expansion and infill is part of a historically "normal" dynamic, versus a problematic departure condition. In the absence of this more holistic understanding, colonization of shrublands by trees tends to be widely regarded as "invasive", even though at least some of these recently colonized areas appear to be an important component of Pinyon Jay habitat in the Great Basin. Achieving this broader perspective may be a necessary prerequisite to successfully accommodating the needs of

706	Greater Sage-Grouse, Pinyon Jays, and other sensitive shrubland and woodland bird species
707	within the overall framework of pinyon-juniper woodland management.
708	
709	Ultimately, accruing information about Pinyon Jays must be incorporated into woodland
710	management paradigms and protocols in the Great Basin (see Ricca et al. [89] for an example) in
711	ways that accommodate both previously-identified and newly-emerging goals within the context
712	of healthy ecosystem function [90]. For the present, Somershoe et al. [15] provide guidance for
713	managers seeking to incorporate Pinyon Jay conservation measures into their vegetation
714	management projects based the extent of current knowledge.
715	
716	
717	Acknowledgments (level 1 heading)
718	
719	Field work was conducted by Gustavo Gonzalez, Michael Maples, and John B. Free (in Eastern
720	Nevada), by Murrelet Halterman, Natasha Peters, Larry Teske, and Mercer Owen (in Southern
721	Idaho, and by Mercer Owen and Sue Brunner (in Central Nevada). Their efforts, which were
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723	Juniper Simonas of Dapper Stats (<u>www.dapperstats.com</u>).
724	
725	Wallace Keck, Superintendent of City of Rocks National Reserve and Park Manager for Castle
726	Rock State Park, provided us with extensive information about local Pinyon Jay populations,
727	generously allowed us use of park facilities, with further assistance from Trenton Durfee. Many
728	local landowners permitted us to access to their property, notable among them LeAnn and Kim

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730	the Bureau of Land Management, Sandra Brewer and John Wilson provided invaluable
731	assistance and support in Central Nevada. We thank all of these individuals.
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Supporting Information Captions

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S1 Table. All data used for data visualizations, ordinations, and logistic regression 1089 analysis, as summarized in Table 2. Each record refers to either a behavior-specific Pinvon 1090 Jay location or a control site. Each record includes various locational and data category 1091 attributes, including decimal latitude and longitude, along with all habitat attributes 1092 1093 considered for inclusion in analysis, as described in Table 2. All attribute headers are sufficiently explicit to be self-explanatory when viewed in conjunction with Table 2. 1094 Definitions of codes for habitat types (which were not used in any analysis or data 1095 1096 visualization) are available in Alexander 1988 [60]. Missing data are intrinsic to the FIA data set. 1097













