



RESEARCH ARTICLE

Variation in home-range size of Black-backed Woodpeckers

Morgan W. Tingley,^{1,2*} Robert L. Wilkerson,² Monica L. Bond,² Christine A. Howell,³ and Rodney B. Siegel²

¹ Woodrow Wilson School, Princeton University, Princeton, New Jersey, USA

² The Institute for Bird Populations, Point Reyes Station, California, USA

³ USDA Forest Service, Pacific Southwest Region, Vallejo, California, USA

* Corresponding author: morgan.tingley@uconn.edu

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ABSTRACT

The Black-backed Woodpecker (*Picoides arcticus*) is a species of conservation concern that is strongly associated with recently burned forests. Black-backed Woodpeckers are known to have variable home-range sizes, yet the ecological factors related to this variation have not been adequately explored and may hold insights into the natural history of the species and the management of its habitat. During 2011 and 2012, we radio-tracked Black-backed Woodpeckers nesting in 3 forested areas of California that burned between 2 and 5 years before the initiation of tracking. Among 15 individuals with robust tracking data, we found that home-range size varied by an order of magnitude, from 24.1 to 304.1 ha, as measured by movement-based kernel estimation. Using an information-theoretic approach, we evaluated the functional relationship between snag basal area—an a priori key resource—and home-range size, additionally controlling for sex, age, and years since fire as covariates. We found that snag basal area alone best predicted home-range size, explaining 54–62% of observed variation. As snag basal area increased, home-range sizes exponentially decreased. This relationship held true both with and without the inclusion of 3 individuals that nested in burned forest yet foraged predominantly outside the fire perimeter in unburned forest. Snag basal area, unlike other potential influences on home-range size, is an attribute that forest managers can directly influence. We describe a quantitative relationship between home-range size and snag basal area that forest managers can use to predict Black-backed Woodpecker pair density in burned forests and assess the likely population consequences of specific harvest treatments. Given that the birds in our study, foraging primarily in burned forest, all had home ranges with an average snag basal area $\geq 17 \text{ m}^2 \text{ ha}^{-1}$, this may represent a benchmark for minimum habitat needs in postfire stands.

Keywords: Black-backed Woodpecker, burned forest, fire, home range, overlap, *Picoides arcticus*, snag basal area, space use

Variation de la taille du domaine vital chez *Picoides arcticus*

RÉSUMÉ

Picoides arcticus est une espèce préoccupante sur le plan de la conservation qui est fortement associée aux brûlis récents. On sait qu'elle a des domaines vitaux de taille variable, mais les facteurs écologiques reliés à cette variation n'ont pas été explorés adéquatement et pourraient ouvrir des perspectives sur l'histoire naturelle de l'espèce et la gestion de son habitat. En 2011 et 2012, nous avons mené un suivi télémétrique de *P. arcticus* nichant dans 3 régions forestières de la Californie qui ont brûlé de 2 à 5 ans avant le début du suivi. Parmi les 15 individus ayant des données télémétriques robustes, nous avons trouvé que la taille du domaine vital variait selon un ordre de magnitude de 24,1 à 304,1 ha, tel que mesuré par une estimation des mouvements par la méthode du noyau. À l'aide d'une approche de la théorie de l'information, nous avons évalué la relation fonctionnelle entre la surface terrière des chicots – à priori une ressource-clé – et la taille du domaine vital, en tenant compte du sexe, de l'âge et du nombre d'années depuis le feu comme covariables. Nous avons trouvé que la surface terrière des chicots seule prédisait le mieux la taille du domaine vital, expliquant 54–62 % de la variation observée. Lorsque la surface terrière des chicots augmentait, la taille du domaine vital diminuait de façon exponentielle. Cette relation était vraie avec et sans l'inclusion de 3 individus qui nichaient dans un brûlis mais qui s'alimentaient surtout à l'extérieur du périmètre du feu dans une forêt non brûlée. La surface terrière des chicots, contrairement aux autres influences potentielles sur la taille du domaine vital, est une caractéristique que les gestionnaires forestiers peuvent influencer directement. Nous décrivons une relation quantitative entre la taille du domaine vital et la surface terrière des chicots que les gestionnaires forestiers peuvent utiliser pour prédire la densité des couples de *P. arcticus* dans les brûlis et évaluer les conséquences démographiques possibles des traitements de récolte spécifiques. Étant donné que les oiseaux dans notre étude, qui s'alimentaient surtout dans les brûlis, avaient tous des domaines vitaux dont la surface terrière des chicots était $\geq 17 \text{ m}^2 \text{ ha}^{-1}$, ceci pourrait représenter une référence pour les besoins minimaux en matière d'habitat dans les peuplements après feu.

Mots-clés: brûlis, feu, domaine vital, chevauchement, *Picoides arcticus*, surface terrière des chicots, utilisation de l'espace



FIGURE 1. Black-backed Woodpeckers in California use heavily burned snags for both nesting and foraging, extracting wood-boring beetle larvae that grow in dead trees after fires. Photo by Stephen Shunk.

INTRODUCTION

The home range, which includes defended and undefended areas used by an individual animal over the course of normal daily or seasonal activities (Burt 1943), is a fundamental spatial unit that defines the fine-scale occurrence of a species. Intraspecific variation in home-range size, however, is still largely unquantified for most species (van Beest et al. 2011). Habitats with more abundant resources are expected to hold individuals with smaller home ranges, and, to the extent that adjacent home ranges do not overlap, areas where individuals have smaller home ranges will generally support higher population densities (Anich et al. 2010). Understanding factors that drive variation in home-range size and population density can yield important insights about the ecology, life history, and conservation of organisms and may suggest more effective management strategies for species of management concern (van Beest et al. 2011, Fieberg and Börger 2012).

One such species of management concern is the Black-backed Woodpecker, which is a designated Management Indicator Species for dead trees, or snags, in burned forest across 10 national forest units in California (Figure 1). At this writing, Black-backed Woodpecker populations in California, Oregon, and the Black Hills of South Dakota are under review for federal listing as threatened or endangered. Black-backed Woodpeckers are strongly associated with recently burned conifer forests (Hutto 1995, 2008, Kotliar et al. 2002, Smucker et al. 2005), where they forage on the larvae of wood-boring beetles that often colonize postfire forests in large numbers (Villard and Beninger 1993, Murphy and Lehnhausen 1998). Use of

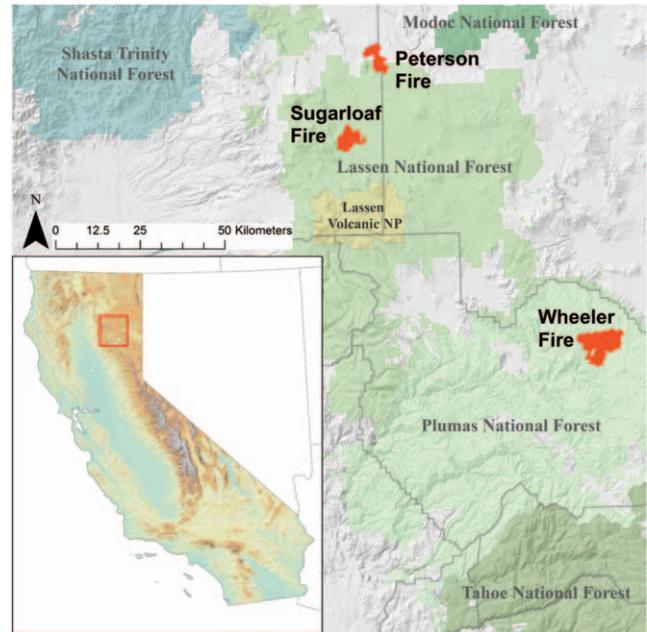


FIGURE 2. Location of the Peterson, Sugarloaf, and Wheeler fire areas in California where Black-backed Woodpeckers were radio-tracked in 2011 and 2012.

postfire forests is rather ephemeral, with local populations of Black-backed Woodpeckers spiking to peak density within the first few years after fire and then declining rapidly within 5–10 yr (Saab et al. 2007, Saracco et al. 2011) or, in some cases, even sooner (Nappi and Drapeau 2009). This decline is presumed to result from the deterioration of a key resource, the snags that provide both nesting opportunities and foraging substrate.

In western forests, the early postfire forest stands that are colonized at high density by Black-backed Woodpeckers are frequently targeted for salvage logging or other management actions that may reduce habitat suitability for the species (Koivula and Schmiegelow 2007, Cahall and Hayes 2009, Saab et al. 2009). We need more information on home-range size, and a better understanding of factors that drive variation in home-range size, so that land managers can make predictions about population size in postfire forests and assess quantitatively the likely consequences that specific plans for salvage logging or other postfire forest treatments may have on those populations.

Here, we explore variation in home-range size and overlap of Black-backed Woodpeckers nesting in 3 burned montane forests of northern California (Figure 2). Black-backed Woodpecker home-range size has never been empirically estimated in California. Elsewhere in the species' range, Black-backed Woodpeckers have relatively large home ranges, typically >100 ha (Goggans et al. 1989, Dudley and Saab 2007, Tremblay et al. 2009, Rota et al.

2014). However, size appears to vary with habitat type and time since fire (Dudley and Saab 2007, Rota et al. 2014). As populations of wood-boring beetle larvae decrease during the years after fire (McCullough et al. 1998), it is believed that Black-backed Woodpeckers enlarge their home ranges before eventually abandoning individual burned areas altogether (Dudley and Saab 2007, Rota et al. 2014).

We developed the present study to address current information needs for Black-backed Woodpecker conservation and burned-forest management. Our primary objectives included (1) estimating the home-range size of Black-backed Woodpeckers nesting in burned forest stands of California and comparing the results to those of previous studies conducted in other forest types and locations; (2) modeling the relationship between home-range size and snag basal area, controlling for covariates of sex and age of birds and time since fire; and (3) measuring the extent of overlap between home ranges of neighboring Black-backed Woodpeckers, which influences pair density across the landscape. The implications of our results are discussed in the context of setting habitat-retention targets that balance the needs of Black-backed Woodpeckers with other forest management objectives.

METHODS

Study Area

We studied Black-backed Woodpeckers occupying areas burned by 3 fires on the Lassen and Plumas national forests, California (Figure 2). These 3 fires—Peterson, Sugarloaf, and Wheeler—had prior survey data indicating high densities of Black-backed Woodpeckers (Saracco et al. 2011) and absence of ongoing logging activity. The 3 study areas ranged from 2–5 yr postfire at the time of study. The Peterson fire burned in 2008, affecting 1,161 ha of mostly eastside pine forest (dominated by *Pinus ponderosa*, *P. jeffreyi*, and *Calocedrus decurrens*, as well as *Quercus kelloggii*). The Sugarloaf fire burned in 2009, affecting 3,129 ha of mostly Sierra mixed conifer forest (consisting mainly of *P. ponderosa*, *P. jeffreyi*, *Abies concolor*, and *C. decurrens*). The Wheeler fire burned in 2007, affecting 9,265 ha of mostly Sierra mixed conifer forest (predominantly *P. ponderosa*, *P. jeffreyi*, and *A. magnifica*). The Peterson fire had the lowest percentage of its area classified as high-severity fire (9.8%), followed by Wheeler (52.6%) and Sugarloaf (53.2%). Two years following the Peterson fire (but before the present study), ~100 ha of forest—mostly in high-severity burned areas—were salvage logged. At the Sugarloaf and Wheeler study areas, postfire snag removal prior to our study was limited to small-scale wood cutting and hazard-tree removal along roads and in a few small, isolated harvest areas.

Data Collection

In late April of 2011 (Peterson and Sugarloaf fires) and 2012 (Wheeler fire), Black-backed Woodpeckers were located and captured either through luring into mist nets or in hoop nets at nest cavities. Birds were only captured exiting nests, starting a minimum of 5 days after egg hatching, to prevent nest abandonment. Only 1 member of each mated pair was tracked for home-range estimation.

We attached a 2.0-g Model BD-2 radio-transmitter (Holohil Systems, Carp, Ontario, Canada) to the dorsal surface of 1 of the inner rectrices of each captured bird. Transmitters were custom modified by the manufacturer with a hole drilled into the large end, through which monofilament was threaded. We used ethyl cyanoacrylate to glue transmitters to a feather shaft and then additionally secured them with 2 loops of monofilament tied around the feather shaft. Birds were aged on the basis of plumage (Pyle 1997) as second-year (SY), third-year (TY), or after-third-year (ATY).

Attempts were made to track marked birds approximately every second day, weather permitting, alternating morning and afternoon. Tracking was conducted using radio receivers and Model RA-7 antennas (Telonics Telemetry Consultants, Mesa, Arizona, USA; AVM Instruments Company, Colfax, California, USA). Teams of 2 observers would visit the perceived home range of a marked bird, use a receiver and antenna to find a signal, and use the homing method (Mech 1983, White and Garrott 1990) to approach and visually locate the bird. Black-backed Woodpeckers were unwary of human observers and consistently allowed trackers to approach within 3–4 m without obviously altering their behavior (Tremblay et al. 2009). Once a bird was visually located, each team would follow it for ≥ 1 hr of continuous tracking or until 20 consecutive foraging locations were marked. Foraging locations were identified with prenumbered vinyl pin flags and a global positioning system (GPS).

Near the end of the field season, we used the radio-tracking data to construct preliminary minimum convex polygons (MCPs) describing each marked bird's observed home range. Within each home range, we defined a systematic grid of points 200 m apart to describe "available" habitat. To effectively cover several very large home ranges at the Peterson fire, the spacing of 28% of Peterson's background grid was expanded to 275 m between adjacent sampling points. The full grid across all 3 fires totaled 977 background grid points covering 2,925 ha (mean points per MCP = 66 ± 39 SD). At every foraging location and background point, we estimated the basal area of snags and live trees using a slope-compensating angle gauge (SEC, Sedona, Arizona, USA). Although other studies have sometimes assessed Black-backed Woodpecker habitat in terms of fire severity (Smucker et al. 2005, Hanson and North 2008), we

considered that a ground-based assessment of snag basal area would provide a more accurate assessment of resource availability for the species. We expect that Black-backed Woodpeckers likely respond more directly to the absolute amount of foraging substrate available, rather than to the proportion of the stand that has been killed by fire. Focusing on snag basal area has the additional benefit of relating home-range size to a metric that is strongly relevant to guiding postfire management.

Across both years and all 3 fires, we radio-tagged and tracked a total of 19 Black-backed Woodpeckers. All the birds nested within the sampled fires, and none of the selected birds shared a nest. We attempted to track all birds until late July, generally well after their nesting attempts were completed, but some birds shed their radio transmitters early, such that the number of recorded foraging locations per bird ranged from 7 to 366. To select which individuals had enough foraging locations recorded to robustly estimate home-range size, we modeled home-range-size convergence using bootstrapping (see Appendix A). Following bootstrapping, we reduced our sample size to 15 birds, each with a minimum of 70 foraging points (mean = 199).

Estimation of Home-range Size

Classically, a home range has been estimated by simply circumscribing all tracked points with an MCP (Mohr 1947), but MCPs are well known to overestimate the areas used by animals, particularly in comparison to more accurate, kernel-based approaches (Cumming and Cornéllis 2012). We present MCP home-range sizes here only to compare our home-range estimates to those of previous Black-backed Woodpecker studies (Goggans et al. 1989, Dudley and Saab 2007, Tremblay et al. 2009). The values reported in the results are means \pm SD.

The second home-range estimator we used, Brownian bridge kernel, accounts for the temporal autocorrelation present in most tracking data. Brownian bridges estimate a utilization distribution (UD) that, in addition to locations of known occurrence, accounts for both the path taken between consecutive relocations and the amount of time between successive observations (Horne et al. 2007a). The Brownian bridge method assumes that the area between consecutive relocations is part of the “home range” and that the degree to which this in-between area is used is related to the amount of time spent traveling between 2 points (in relation to the speed of the animal). More information on the parameterization and modeling of Brownian bridge home ranges is presented in Appendix B. Throughout the present study, we present Brownian bridge kernel home ranges evaluated at 2 percentiles: the 50th percentile (or “core kernel” home range) and the 95th percentile (or “full kernel” home range). All home-range metrics were calculated in R (R Core Team 2013)

and made use of the packages “adehabitatHR” and “adehabitatLT” (Calenge 2006).

Analysis of Home-range Size and Overlap

Of particular interest was the resource availability within home ranges. We estimated basal area (converted to $\text{m}^2 \text{ha}^{-1}$) of stands surrounding all foraging locations and background points, then used these data to interpolate a constant surface of snag and live-tree basal area within each of the 3 fire areas. Using the Spatial Analyst extension of ArcGIS version 9.3 (ESRI, Redlands, California, USA), we interpolated continuous basal-area surfaces with the inverse distance weighting method parameterized with 10 points and a maximum distance of 500 m to create a 50×50 m resolution surface. We then clipped surfaces to the MCP, core, and full kernel home ranges for each bird and calculated the mean and standard deviation of snag and live-tree densities.

We used a multimodel framework (Burnham and Anderson 2002) to determine the appropriate functional form and relationship of snag basal area to home-range size across the sample of birds with robust estimates. We used generalized linear models to initially test 4 different forms of the snag basal area–home range relationship: a linear model ($y = \beta_0 + \beta_1 x$), a quadratic model ($y = \beta_0 + \beta_1 x + \beta_2 x^2$), a log-linear model [$\ln(y) = \beta_0 + \beta_1 x$], and an intercept-only model ($y = \beta_0$). The 4 model forms represent different biological hypotheses: (1) that the rate of change in home-range size with snag basal area is constant (linear); (2) that the rate of change in home-range size with snag basal area shifts somewhere from positive to negative (quadratic); (3) that the rate of change in home-range size with snag basal area decreases incrementally to zero (log-linear); and (4) that there is no relationship between snag basal area and home-range size. An additional model, a broken-line or threshold model, was attempted, but no breakpoints were found within the range of sampled snag densities, indicating a lack of a clear threshold. Models were compared using Akaike’s Information Criterion corrected for small samples sizes (AIC_c ; Burnham and Anderson 2002). Following this comparison, we tested 3 additional models, adding covariates to the best model of snag basal area previously identified: (5) age of fire + snag basal area; (6) age of bird + snag basal area; and (7) sex of bird + snag basal area. Covariates were added to test for confounding effects on the snag basal area relationship. We ranked all 7 models for each home-range estimator using AIC_c and compared the ability of each model to explain observed variation with r^2 .

In addition to absolute home-range size, we were interested in the overlap between neighboring home ranges. Because we were unable to capture and track all potential neighboring birds within each fire, our analysis focused on the extent of observed overlap among the 15

robustly sampled birds rather than a summary of total overlap. For each pair of neighboring home ranges, we calculated the percentage of a bird's MCP area that overlapped with its neighbor's. Recognizing that MCPs often overestimate overlap as a result of their lack of concavity and the assumption of equal use within the home range (Kernohan et al. 2001), we calculated 2 additional kernel-based metrics following the recommendations of Fieberg and Kochanny (2005). We used the full (95th percentile) kernel home range to estimate both the probability of home-range overlap between every pair of birds (PHR) and the Utilization Distribution Overlap Index (UDOI). Both indices take into account uneven space use within home ranges, as defined by the kernel density estimate of the UD. The UDOI, which equals zero for 2 nonoverlapping ranges and 1 for perfectly overlapping ranges with uniformly distributed use, is recommended as the most appropriate measure for quantifying overlap in terms of space-use sharing (Fieberg and Kochanny 2005). Percent MCP overlap and PHR are calculated with respect to 1 half of a 2-bird pair, whereas UDOI is a metric given identically to both pair halves.

RESULTS

Home-range Estimation

Of the 15 birds with sufficient radio-tracking data for estimating home-range size (see Appendix A), 10 were males and 5 were females. Five of these birds (4 males and 1 female) nested in the Peterson fire, 1 bird (male) nested in the Sugarloaf fire, and 9 birds (5 males and 4 females) nested in the Wheeler fire. Combined across all fires, data from these 15 birds consisted of 255 bouts of 2,992 observed foraging events. The MCP and Brownian bridge kernel methods provided estimation of home-range sizes with qualitatively different results (Figure 3 and Table 1). As expected, MCPs gave larger estimates of home-range size (33–796 ha; mean = 204 ± 233 ha), whereas full kernels gave more conservative home-range sizes (24–304 ha; mean = 89 ± 75 ha). Independent of estimation method, there was a wide range in home-range sizes, with 3 birds (P1, P3, and P5) exhibiting home ranges 2–3 times greater than the overall mean and approximately an order of magnitude greater than the smallest home ranges we estimated. For the 15 birds, there was no statistically significant correlation between home-range size and the number of foraging points (MCP: $r = 0.39$, $P = 0.15$; full kernel: $r = 0.46$, $P = 0.08$; core kernel: $r = 0.38$, $P = 0.16$) or bouts (MCP: $r = 0.51$, $P = 0.05$; full kernel: $r = 0.44$, $P = 0.10$; core kernel: $r = 0.32$, $P = 0.24$) measured.

Resource Availability within Home Ranges

Mean snag basal area of full kernel home ranges varied between 3.2 and $35.7 \text{ m}^2 \text{ ha}^{-1}$ (median = $20.1 \text{ m}^2 \text{ ha}^{-1}$), and

mean live-tree basal areas varied between 3.6 and $35.0 \text{ m}^2 \text{ ha}^{-1}$ (median = $12.8 \text{ m}^2 \text{ ha}^{-1}$). Much of this variation was explained by 3 of 15 birds (P3, P5, and P6), all nesting within the perimeter of the Peterson fire, that foraged extensively in the surrounding unburned forest. With the exception of these 3 birds, all home ranges had mean snag basal areas $\geq 17 \text{ m}^2 \text{ ha}^{-1}$ and mean live-tree basal areas $< 19 \text{ m}^2 \text{ ha}^{-1}$. For all birds, however, average snag densities within core kernels were significantly higher (paired t -test: $t_{14} = 3.6$, $P = 0.003$) and live-tree densities were significantly lower (paired t -test: $t_{14} = -2.4$, $P = 0.03$) than within full kernels.

We used the ratio of mean snag basal area to live-tree basal area to explore the relative abundance of snags versus live trees within each bird's home range. Within full kernel home ranges, the ratio of snags to live trees was > 1 (indicating relatively more snags than live trees) for all 12 primarily burn-foraging birds (Table 1). This ratio reached a maximum of nearly 10:1 for W8, which occupied a particularly high-severity portion of the Wheeler fire. For the 3 birds that foraged extensively in unburned forest, the ratio was < 1 .

The 3 birds that foraged extensively in unburned forest showed strongly different habitat–space use patterns than the other 12 tracked birds. Although all birds nested within the fire perimeter, these 3 birds nested peripherally—within 120 m of the fire edge—whereas the other birds' nests ranged from 318 to 2,554 m from the fire edge. For P3, P5, and P6, 89%, 45%, and 93%, respectively, of each bird's observed foraging points were outside the fire perimeter, with the farthest foraging observation 5.49 km from the bird's nest. Even when outside the fire perimeter, these 3 birds continued to forage primarily ($> 75\%$ of observations) on dead or ailing trees.

Predictors of Home-range Size

We found a strong negative relationship between average snag basal area and home-range size (Figure 4). Evidence from a multimodel comparison best supported a log-linear relationship of snag basal area to home-range size over linear and quadratic forms (Table 2; for full kernel log-linear model, parameter means \pm SE: intercept = 4.23 ± 0.24 , slope = -0.59 ± 0.16). This model indicated that as snag basal area increased, the marginal change in home-range size decreased monotonically. Other covariates, including years since fire, sex of bird, and age of bird, provided no additional inferential support (i.e. lower ΔAIC_c) to a model including only mean snag basal area (Table 2), and ΔAIC_c values of these additional models were nearly all greater than what one would expect by adding 1 additional, random parameter (i.e. $\Delta\text{AIC}_c > 1.82$; Arnold 2010). For full kernel home ranges, the parameters for fire age ($\beta_{\text{fire.age}} = -0.25 \pm 0.19$), bird age ($\beta_{\text{SY}} = 0.01 \pm 0.32$, $\beta_{\text{TY}} = 0.14 \pm 0.59$), and sex of bird ($\beta_{\text{male}} = -0.49 \pm 0.46$)

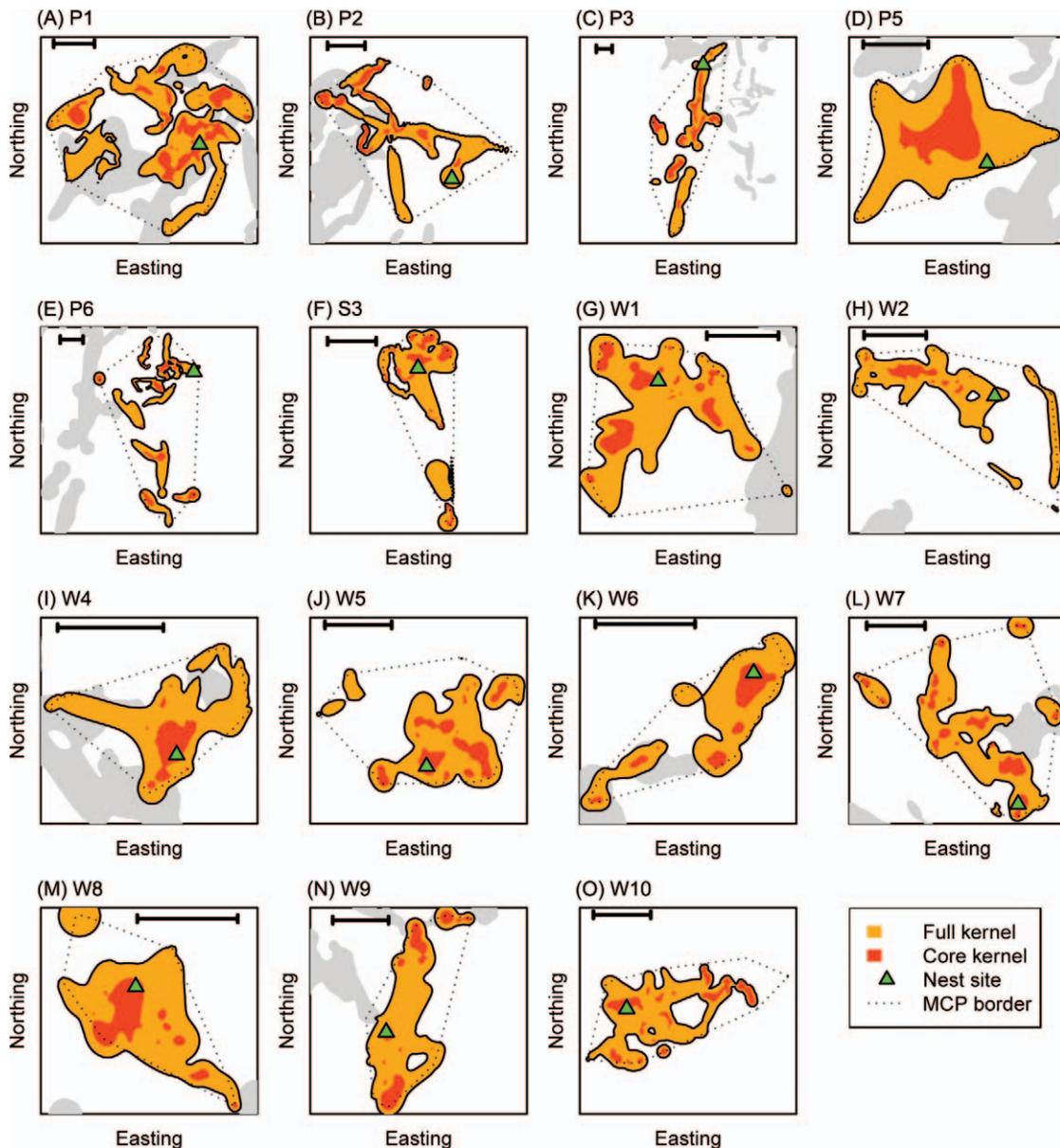


FIGURE 3. Maps of home-range size for radio-tracked Black-backed Woodpeckers, with robust estimates at the Peterson (A–E), Sugarloaf (F), and Wheeler (G–O) fires, as estimated by MCP (dotted outline) and Brownian bridge kernels (colors). Maps additionally indicate full kernel home ranges of other nearby radio-tracked birds (gray background) and nest locations (green triangles). Scale bars represent 500-m increments.

all had 95% confidence intervals that overlapped zero, and results were inferentially similar for other home-range estimates. Thus, we do not consider age of fire, sex of bird, or age of bird to be competitive predictors of home-range size, as based on model deviance (Burnham and Anderson 2002). Log-linear models of snag basal area explained 54–62% of the measured variation in home-range size across the 15 birds with robust estimates (Table 2).

Although the 3 birds that foraged extensively in unburned forest (P3, P5, and P6) had relatively larger

home ranges, these 3 data points did not drive the significant relationship between home-range size and average snag basal area. Removing the 3 birds barely changed coefficient estimates for snag basal area for the MCP model (change in coefficient = -0.02) or the full kernel model (change = -0.01) and resulted in a steeper slope for the core kernel model (change = -0.27). For all models, the inclusion of the 3 birds reduced standard errors of slope coefficients by 0.14, 0.19, and 0.14, respectively, thus increasing model precision.

TABLE 1. Home-range size estimates (HR) and habitat characteristics for each of 15 Black-backed Woodpeckers, based on Brownian bridge kernel and minimum convex polygon (MCP) estimation methods.

Bird ^a	Sex	Age ^b	Core kernel HR (ha) ^c	Full kernel HR (ha) ^c	MCP HR (ha) ^c	Snag basal area (m ² ha ⁻¹) ^d	Live-tree basal area (m ² ha ⁻¹) ^d	Ratio of snags to live trees ^d
P1	F	ATY	31.8	184.5	366.9	18.2	13.8	1.32
P2	M	TY	15.4	101.6	299.7	18.3	14.2	1.29
P3	M	SY	64.6	304.1	795.8	3.2	28.4	0.11
P5	M	SY	20.6	88.1	108.8	4.4	23.5	0.19
P6	M	ATY	22.9	161.7	594.0	4.9	35.0	0.14
S3	M	SY	7.7	50.7	84.9	31.4	12.0	2.62
W1	M	ATY	11.2	66.3	120.7	31.6	9.4	3.37
W2	F	TY	3.7	43.8	122.0	29.8	8.8	3.39
W4	F	ATY	3.4	24.1	35.8	20.9	11.1	1.88
W5	M	ATY	11.1	56.6	107.2	19.7	18.4	1.07
W6	M	SY	4.0	24.5	33.4	28.1	6.5	4.30
W7	M	SY	10.6	67.4	166.5	17.4	15.7	1.11
W8	F	ATY	6.1	34.9	39.5	35.7	3.6	9.81
W9	M	ATY	10.5	67.8	93.1	20.1	12.8	1.57
W10	F	SY	9.1	57.1	96.4	35.0	8.1	4.32

^a First letters of bird codes designate fire (P = Peterson, S = Sugarloaf, W = Wheeler).

^b Age classes: SY = second-year, TY = third-year, and ATY = after-third-year.

^c Core kernels are defined by the 50th percentile; full kernels are defined by the 95th percentile; MCP home ranges are defined by the 100th percentile.

^d Based on mean habitat measurements within the full kernel home range.

Home-range Overlap

Some degree of overlap in home range was detected for 7 pairs of robustly tracked birds. For these 7 pairs, the amount of overlap varied considerably (Table 3), with estimates highly dependent on metric. The percentage of MCP area overlap was greatest for W4 (88.5% with W7) and P5 (81% with P1), but all other pairings showed overlap of <25% of the home-range area. The MCPs include unused space (if home ranges are concave) as well as little-used space (e.g., cross-territory forays), so they are

expected to overestimate overlap. By contrast, overlap statistics derived from kernel UD's indicated high spatial segregation (i.e. low overlap of areas with the greatest use) of home ranges (Table 3 and Figure 3), even for those individuals with high MCP overlap. The PHR scores, indicating the probability that 2 birds occupy a portion of the same home range, were <20% for all but 1 pairing. The UDOI scores, where perfect overlap and homogeneous spatial use gives a score of 1, were <0.05 for all birds.

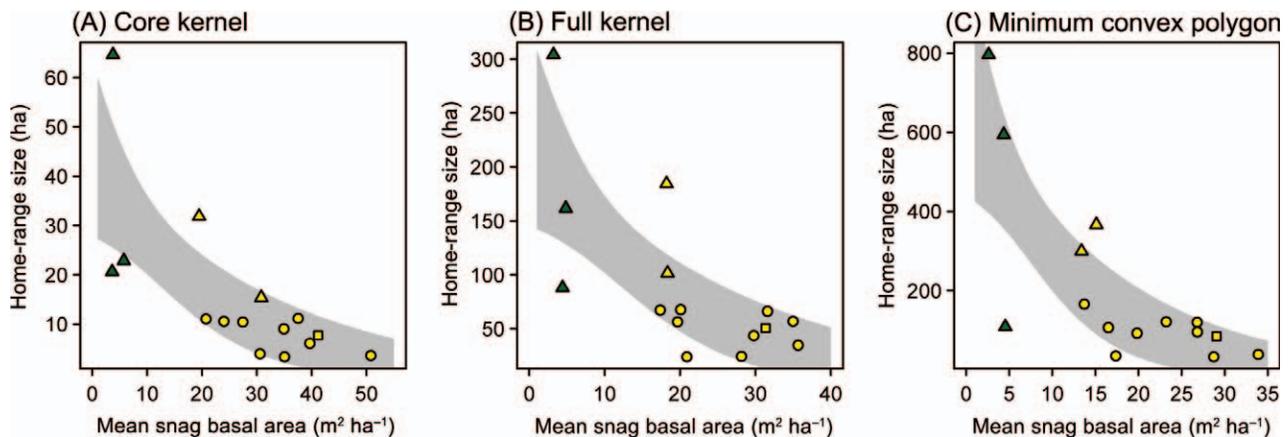


FIGURE 4. Relationship between mean snag basal area (m² ha⁻¹) and Black-backed Woodpecker home-range size for each of 3 home-range estimations (A–C). Data are presented for birds tracked in 3 fires (triangles = Peterson, square = Sugarloaf, and circles = Wheeler) and differentiate between birds foraging extensively in burned forest (yellow) versus unburned forest (dark green). The model is presented as 95% confidence interval around the best-supported model explaining home-range variation as a function of snag basal area (see Table 2).

TABLE 2. Difference in AIC_c values (Akaike's Information Criterion corrected for small sample size) and associated statistics comparing different models of variability in Black-backed Woodpecker home-range size.

Home-range estimator	Model	K	ΔAIC_c	w_i	r^2
Core kernel ^a	Snag basal area (log-linear)	3	0	0.70	0.56
	Snag basal area (linear)	3	1.56	0.15	0.51
	Snag basal area (log-linear) + sex of bird	4	2.21	0.08	0.61
	Snag basal area (log-linear) + fire age	4	2.33	0.07	0.60
	Snag basal area (quadratic)	4	3.85	0.01	0.56
	Snag basal area (log-linear) + age of bird	5	7.70	0.00	0.58
	Intercept-only	2	11.28	0.00	0.00
Full kernel ^b	Snag basal area (log-linear)	3	0	0.70	0.54
	Snag basal area (log-linear) + fire age	4	1.73	0.12	0.60
	Snag basal area (linear)	3	1.87	0.11	0.48
	Snag basal area (log-linear) + sex of bird	4	2.66	0.05	0.57
	Snag basal area (quadratic)	4	3.68	0.02	0.54
	Snag basal area (log-linear) + age of bird	5	8.41	0.00	0.54
	Intercept-only	2	8.42	0.00	0.00
MCP ^c	Snag basal area (log-linear)	3	0	0.86	0.62
	Snag basal area (log-linear) + fire age	4	2.56	0.07	0.65
	Snag basal area (log-linear) + sex of bird	4	3.14	0.04	0.64
	Snag basal area (linear)	3	3.71	0.02	0.51
	Snag basal area (quadratic)	4	4.36	0.01	0.60
	Snag basal area (log-linear) + age of bird	5	6.55	0.00	0.67
	Intercept-only	2	9.22	0.00	0.00

^a Minimum AIC_c score = 119.9.

^b Minimum AIC_c score = 167.7.

^c Minimum AIC_c score = 197.4.

DISCUSSION

Black-backed Woodpecker home ranges within our 3 fires varied by approximately an order of magnitude, and this variation was explained in large part by a single resource characteristic: mean snag basal area. Both Dudley and Saab (2007) and Rota et al. (2014) found that Black-backed Woodpeckers in burned forests increased their home-range size with increasing years postfire. In the birds we studied, neither time since fire nor several other possible covariates provided additional explanatory power beyond the relationship with snag basal area. Unlike time since fire, snag basal area is a habitat attribute that forest managers can directly influence. Our results suggest that postfire stands with high snag basal area may support many more Black-backed Woodpeckers than stands with low snag basal area.

Foraging in Unburned Forest

Perhaps our most surprising result is the finding that 3 of the focal birds (P3, P5, and P6) had home ranges that encompassed large amounts of unburned forest outside the fire perimeter. The 2 birds that foraged in unburned areas the most frequently had home ranges substantially larger than those of any of the other tracked birds—a fact that strengthened but did not solely account for the relationship between snag basal area and home-range size.

TABLE 3. Overlap statistics for the 7 pairs of Black-backed Woodpecker that showed nonzero home-range overlap.

Bird 1 ^a	Bird 2 ^a	Percent MCP overlap	PHR score ^b	UDOI score ^c
P1	P2	18.2	14.3	0.023
P2	P1	22.3	19.3	–
P1	P3	14.5	5.7	0.001
P3	P1	6.7	2.5	–
P1	P5	24.1	8.9	0.026
P5	P1	81.4	35.4	–
P3	P6	5.1	0.2	<0.001
P6	P3	6.8	0.5	–
W1	W9	6.7	1.0	<0.001
W9	W1	8.7	1.0	–
W4	W7	88.5	18.1	0.035
W7	W4	19.1	15.7	–
W6	W9	17.6	13.5	0.018
W9	W6	6.3	13.0	–

^a Overlap was measured across all robustly radio-tracked birds but is presented here for only those pairs of individuals with nonzero overlap. The minimum convex polygon (MCP) and probability of home-range overlap (PHR) statistics are based on overlap for bird 1 of a pair. The Utilization Distribution Overlap Index (UDOI) scores are unique to the pair.

^b PHR measures the probability (%) that any other bird co-occurred within the 95% kernel home range of a focal individual according to the modeled utilization distributions (UDs).

^c UDOI is a metric that uses UD to robustly compare space use of 2 individuals. The metric has a value of zero for nonoverlapping individuals and a value of 1 for fully overlapping individuals with uniform space use and can be >1 if home ranges show overlapping non-uniform space use.

TABLE 4. Summary of published studies of Black-backed Woodpecker home-range size in comparison to findings presented here.

Study	Home-range size (ha)			Method	Percentile	<i>n</i>	YSF ^a	Location	Period ^b
	Min.	Max.	Mean						
Goggans et al. 1989	72	328	175	MCP	100th	3	–	Oregon	Post-fl.
Dudley & Saab 2007	24	91	45	Fixed kernel	50th	4	6–8	Idaho	Post-fl.
Dudley & Saab 2007	116	421	217	Fixed kernel	95th	4	6–8	Idaho	Post-fl.
Dudley & Saab 2007	124	573	322	MCP	95th	4	6–8	Idaho	Post-fl.
Dudley & Saab 2007	150	766	429	MCP	100th	4	6–8	Idaho	Post-fl.
Tremblay et al. 2009	100	256	151	MCP	100th	8	–	Quebec	Pre-fl.
Rota et al. 2014 ^c	30	187	70	Fixed kernel	99th	11	1	South Dakota	Both
Rota et al. 2014 ^c	20	226	88	Fixed kernel	99th	10	2	South Dakota	Both
Rota et al. 2014 ^c	37	825	439	Fixed kernel	99th	5	3	South Dakota	Both
Rota et al. 2014 ^c	399	416	408	Fixed kernel	99th	2	4	South Dakota	Both
Present study	3	64	16	Movement kernel	50th	15	2–3, 5	California	Both
Present study	24	304	89	Movement kernel	95th	15	2–3, 5	California	Both
Present study	33	796	204	MCP	100th	15	2–3, 5	California	Both

^a Years since fire, if applicable.

^b “Pre-fl.” indicates that data were collected prior to nestlings fledging; “Post-fl.” indicates that data were collected after nestlings fledged; “Both” indicates that data were collected before and after fledging.

^c Rota et al. (2014) present home-range estimates for multiple disturbance habitats, including pine-beetle-killed forest and prescribed fire. The home-range sizes presented here are for only those areas burned by wildfire.

All 3 birds were males; P3 and P5 were SY birds, and P6 was ATY.

One key difference in foraging strategies between the burned-forest and unburned-forest foraging birds appeared to be travel distance. During continuous tracking bouts, the unburned-forest birds traveled significantly greater distances between foraging events (mean travel distance in burned forest = 74 m; mean travel distance in unburned forest = 167 m; $P < 0.001$). It is unclear whether this difference has consequences for fitness, competitive ability, or nesting success.

These results lead to interesting questions about how often, under what conditions, and with what productivity consequences Black-backed Woodpeckers may forage across large spatial areas in unburned forest. Although the species is found in California at much higher densities in recently burned forest, it is also uncommonly encountered in unburned forests. The much larger home ranges we observed among the small subset of birds that foraged extensively in unburned forest may suggest that unburned forest provides lower-quality habitat and that Black-backed Woodpeckers that utilize it must occupy larger home ranges to provide adequate foraging opportunities. Smaller home ranges generally allow animals to minimize movement costs, exposure to predators, and territory defense (Adams 2001), although it is unknown how this translates to fitness benefits in birds. Further study of Black-backed Woodpeckers that forage or even nest in unburned forests in the same region would be useful for resolving whether Black-backed Woodpeckers using unburned forest incur a fitness disadvantage.

Size and Characteristics of Home Ranges

Black-backed Woodpecker home-range estimates from outside California have varied substantially, although much of this variation may be due to different home-range estimation methods and conditions during radio-tracking, as well as small sample sizes (Table 4). For example, Dudley and Saab (2007) and Goggans et al. (1989) conducted their studies during the postfledging period, when woodpeckers, at least in some portions of their range, may wander more widely in search of patchy food resources (Tremblay et al. 2009), whereas Tremblay et al. (2009) studied home-range size during the prefledging period. Dudley and Saab (2007) and Rota et al. (2014) are the only studies of home ranges besides our own to have examined Black-backed Woodpeckers within burned forests. Among 3 of the 4 published studies, the 100th-percentile MCP is a common reporting metric, even if its biological meaningfulness has been questioned (Börger et al. 2006). Comparing among 100th-percentile MCP estimates, mean home-range sizes in the 3 previous studies varied from 151 to 429 ha, with the larger number derived from burned forests.

Although our mean 100% MCP home-range size is close to that of Dudley and Saab (2007), our mean is skewed high by the very large MCP home ranges of 2 birds that foraged predominantly outside the fire perimeter (Table 1). A more nuanced comparison suggests that our home ranges are generally smaller than those previously reported; 10 of 15 birds in our study had 100% MCPs smaller than the minimum MCP area of 124 ha in Dudley and Saab (2007). Based on kernel estimates, our home ranges were consistently smaller than those reported in

Dudley and Saab (2007), for both full kernel and core kernel home ranges. In fact, the mean full kernel home range of our 15 birds was less than the minimum 95th percentile kernel home range in Dudley and Saab. The difference in estimates of home-range size could plausibly be due to sampling (Dudley and Saab tracked only 4 birds), region (ecological differences between Idaho and California), resource availability, or time since fire.

Although calculating MCPs provides a useful comparative crosswalk to previous studies, we recommend using kernel-density estimators for ecological inference. In particular, movement-based kernel estimates (e.g., Brownian bridges) are better at dealing with concavity, holes, and noncontinuous home ranges and result in more accurate descriptions of the home range than MCPs or fixed-kernel approaches (Downs et al. 2012, Cumming and Cornélie 2012, Fischer et al. 2013). The “full” (95th percentile) kernel estimate is an established standard metric for comparing home-range estimates across individuals, populations, and species. In comparison, the “core” (50th percentile) kernel estimate provides a comparative region that can be used to investigate how resource–area relationships or resource availability change between the area where an individual spends most of its time and the full area where it occurs (Barg et al. 2006, Anich et al. 2012).

Variation in Home-range Size and Overlap

Home-range sizes of our focal birds varied greatly, exhibiting an exponentially negative relationship with mean snag basal area (Table 1 and Figure 4), regardless of whether the 3 birds that foraged in unburned forest were considered. This high level of individual variation suggests that, even within postfire forest stands that have been selected by Black-backed Woodpeckers, resource availability for the species varies widely. The univariate, quantitative relationship between snag basal area and home-range size may help land managers predict the effects of postfire forest-management strategies on local Black-backed Woodpecker populations by providing quantitative trade-offs—in numbers of expected woodpecker pairs—of treating burned stands with salvage logging or other prescriptions that remove snags. More proactively, the relationship between snag density and woodpecker density can be used to design postfire management plans that retain adequate numbers of snags to support breeding Black-backed Woodpeckers.

Dudley and Saab (2007) suggested that Black-backed Woodpecker home ranges expand within burned forests over time, as snags fall and decomposing trees gradually decline in foraging quality. This hypothesis was recently supported by Rota et al. (2014), who showed substantial increases in home-range size between 1 and 4 yr postfire. Interestingly, our study did not support a strong relation-

ship between fire age and home-range size. Although our sample of postfire years (2–5 yr) was consistent with the 1- to 4-yr time spread of Rota et al. (2014), it still fell short of the nearly decadal postfire period during which Black-backed Woodpeckers are known to inhabit burned forests in California (Saracco et al. 2011). Given that our sampled forests contain a greater diversity of conifers—which may decompose at varying rates—than the nearly monotypic stands of *Pinus ponderosa* sampled by Rota et al. (2014), previously established relationships between home range-size and time since fire may differ in more diverse forests.

Comparing the Peterson fire (3 yr postfire) to the Wheeler fire (5 yr postfire), birds within the Peterson fire had much greater mean home-range areas than Wheeler birds (Table 1), opposite to the pattern expected on the basis of fire age alone (Rota et al. 2014). Factors other than fire age appear to have been more important drivers of home-range size in our study. For one, birds foraging partly outside the burned areas had larger home ranges. The difference in habitat characteristics between the 2 fire areas is also important. The Wheeler fire, although older, has much more extensive high-severity burned areas than the Peterson fire, which includes large patches of forests with relatively few fire-killed trees and which was treated with more postfire logging of the areas that were burned at higher severity. These differences in stand structure and burn severity (i.e. available habitat) may far outweigh potential effects of snag aging on home-range sizes. To robustly study this process, one would need to compare home-range sizes within the same fire from year to year.

Of our 15 focal birds, 5 were female and 10 were male. It is unknown whether male and female Black-backed Woodpeckers have differently sized foraging home ranges during the breeding season or whether there are any systematic differences in foraging behavior. Dudley and Saab (2007) sampled only male woodpeckers. In our study, we found no support for sex of bird as a predictor of home-range size (Table 2). Dudley and Saab (2007) noted that their 4 male birds showed no overlap in home ranges, whereas we noted some overlap but generally segregated use (Table 3). It is difficult to parse overlap by sex in our study. Some female birds (e.g., P1 and W4) had particularly high rates of overlap (with nonmates), yet home-range overlap was also observed between male birds (e.g., W1 and W9).

Implications for Managing Postfire Forests

It has been argued elsewhere that postfire logging is largely incompatible with the maintenance of native biodiversity in severely burned forests (Hutto 2006, Hanson and North 2008). Nevertheless, forest managers often face decisions about which postfire stands to harvest for economic or other purposes (e.g., restoration and replanting) and which stands to retain on the landscape. Our results provide

guidance for selecting retention stands in postfire forests that may be relatively more beneficial to Black-backed Woodpeckers. Black-backed Woodpeckers occupying stands with greater average snag basal area tend to have smaller home ranges. Because overlap in adjacent Black-backed Woodpecker ranges is generally small, at least using the UD-based statistics (Table 3), a postfire stand with high snag basal area is therefore likely to support more Black-backed Woodpecker pairs than a stand of the same area but with lower average snag basal area. Of the 12 individual birds that foraged exclusively or primarily within burned forest, all had full kernel home ranges with an average snag basal area $>17 \text{ m}^2 \text{ ha}^{-1}$ (Table 1). This minimum benchmark of $17 \text{ m}^2 \text{ ha}^{-1}$ could potentially be used by managers seeking to select newly burned forest stands for retention as Black-backed Woodpecker habitat. Although Black-backed Woodpeckers may also occupy areas (including unburned forest adjacent to burned areas) with lower snag densities, retained stands with greater snag basal area are generally likely to support greater numbers of Black-backed Woodpeckers than similar-sized stands with less snag basal area.

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APPENDIX A

Sample Size of Foraging Locations Necessary for Robust Home-range Estimation

How many geographic locations are necessary to robustly estimate a home range has long been a key question in spatial ecology (Odum and Kuenzler 1955). Although radio-tracking study designs aim to gather adequate sample sizes for all individuals, many factors can contribute to why insufficient sample sizes are collected. For example, transmitters can fall off or stop signaling, tracking teams may need to spread their effort across many individuals, and sometimes animals simply disappear.

There is little consensus on how a “robust” sample size for home-range estimation should be measured. How many points are necessary to model a stable home range depends on the biology of the organism (i.e. its temporal movement patterns) and the type of home-range estimator

used. For kernel density estimators, Seaman et al. (1999) recommended a minimum of 30 location points per animal, and preferably >50. Some authors, however, have found little bias to using sample sizes as small as 15 (Anich et al. 2009). A cutoff of 15 points would allow us to use all 19 radio-tracked Black-backed Woodpeckers, but we wanted to ensure that home-range estimates from MCPs as well as Brownian-bridge kernel models were robust.

To assess adequate sample size, we used a bootstrap procedure where, for each bird, increasing numbers of relocation points were drawn at random (without replacement) and used to build an MCP resulting in an area estimate. For each bird, 5 points were randomly drawn at the start of the sequence, and sample sizes increased incrementally until all sample points (n) were drawn. Following Odum and Kuenzler (1955), we then calculated the incremental change in home-range size, with each successive sample point. For each bird, the random drawing of points was repeated 10,000 times, thus allowing the calculation of means and 95% confidence intervals around the incremental change in home-range size with increasing samples (Appendix A, Figure 5). We decided on a conservative cutoff of having 95% confidence intervals converge to <2% incremental change in estimated area.

Based on the results of this sample-size analysis, we excluded 4 birds (P4, S1, S2, and W3) from formal home-range-size analysis because of a lack of convergence of home ranges (Appendix A, Figure 5). Our resulting group of 15 birds each had >75 relocation points. Previous analyses (Seaman et al. 1999, Anich et al. 2009) indicated that this sample size is more than adequate for kernel-based home-range analysis as well as for robust MCP home-range estimates.

APPENDIX B

Expanded Methodology on Estimation of Home-range Size

Introduction to Brownian bridge home-range estimation. A home range can be estimated using various methods, depending on assumptions, data type, and data quality. Classically, home range has been estimated by simply circumscribing all tracked points with an MCP (Mohr 1947), but MCPs are well known to overestimate the areas used by animals, particularly in comparison to more accurate, kernel-based approaches (Huck et al. 2008, Cumming and Cornéllis 2012). Although MCP home ranges have considerable bias, they are important to calculate nonetheless, so as to provide a backward comparison to previous studies (e.g., Goggans et al. 1989, Dudley and Saab 2007, Tremblay et al. 2009).

The home-range method used in the present study is Brownian bridge kernel estimation. Like all kernel methods, Brownian bridge kernel estimation models the

home range of an animal by fitting a spatial probability density around known locations of occurrence. This probability cloud, the utilization distribution (UD), represents the probability that an animal occurred in an area over a specified period (Horne et al. 2007a). With sufficient sampling over relevant periods (e.g., a breeding season), the UD is treated as a good measure of the home range of an individual, generally using the 95th percentile to delineate usage boundaries (Huck et al. 2008, Cumming and Cornéllis 2012).

The Brownian bridge kernel estimator improves upon classical “fixed” kernel estimation in several ways. Fixed kernel estimates assume that all observations of an individual’s location (“fixes”) are completely independent. Whether using GPS or radio telemetry, this assumption is rarely met, because consecutive fixes are almost always serially correlated (Horne et al. 2007b). Serial correlation is also dependent on the time between fixes; although an animal may move only 50 m between consecutive fixes, if the time between fixes is 3 hr, there is more uncertainty about where the individual went than if there is only 3 min between fixes. Although serial correlation and variable time intervals are characteristic of most telemetry data, they greatly violate the assumptions of fixed kernel estimation, resulting in fixed kernel home ranges that can greatly overestimate or underestimate the true home range (Horne et al. 2007b, Downs et al. 2012, Cumming and Cornéllis 2012).

By contrast, Brownian bridge kernel estimation incorporates serial correlation by explicitly using both the path taken between consecutive relocations and the amount of time between observations at successive foraging points (Horne et al. 2007a). By using the order in which tracking data are collected, Brownian bridge estimation includes the area between consecutive relocations as part of the home range but incorporates the degree to which this in-between area is used in relation to the amount of time spent traveling between 2 points (i.e. the speed of the animal). Compared to fixed-kernel methods, Brownian bridge kernels result in complex UD's with multiple areas of high use and areas—often within the home range—with little or no use (Horne et al. 2007a). The inability of fixed-kernel methods to reliably capture holes and movement corridors has been criticized (Getz et al. 2007), because these are common characteristics of animal space use (Getz and Wilmers 2004, Ryan et al. 2006, Horne et al. 2007a). When tested against multiple models of home-range estimation using real home-range data, Brownian bridge kernels reliably produce the most accurate home ranges, balancing sensitivity with specificity (Cumming and Cornéllis 2012). Recently, Brownian bridge estimation has been recommended over fixed kernels specifically for measuring home ranges of birds for all the above reasons (Fischer et al. 2013).

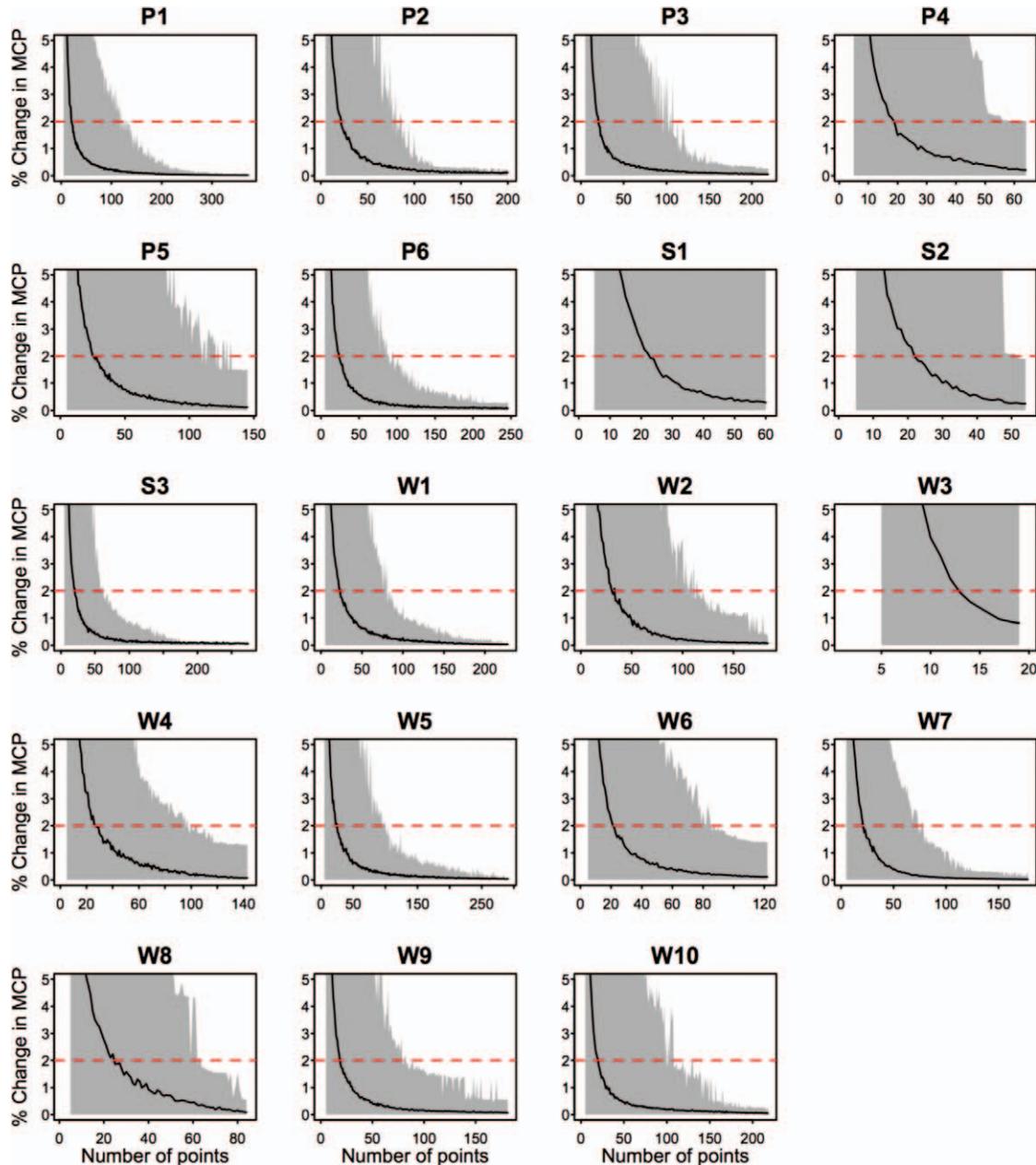


FIGURE 5. Mean (black line) and 95% credible interval (gray) of percent change in MCP home-range size for increasing random draws of n relocation points for each radio-tracked Black-backed Woodpecker. Plots were assessed for evidence of home-range convergence as n increased, signified by a 95% confidence interval converging to $<2\%$ change in MCP with each successive draw.

Modeling of Brownian bridge home ranges for Black-backed Woodpeckers. For each woodpecker, foraging locations and movements were tracked on multiple days. On each tracking day, the woodpecker was followed for ~ 1 hr, or until ≥ 20 foraging locations had been visited, whichever was shorter. Each day of tracking is referred to as a “bout.” Our data showed a median of 10 fixes bout⁻¹. Of the 15 birds with sufficient radio-tracking data (see Appendix A), the number of bouts ranged from 5 to 25,

with a mean of 17. The number of total fixes per bird ranged from 85 to 366, with a mean of 200. To illustrate the process of constructing Brownian bridge home ranges, we use a bird with below-mean sampling, W4, an adult female that was tracked for 12 bouts with 144 fixes (Appendix B, Figure 6).

Movement-based kernel estimation requires tracking points to be ordered temporally with approximate time intervals between points. These time interval data (I_x) were collected during sampling in 2012; but in 2011, elapsed

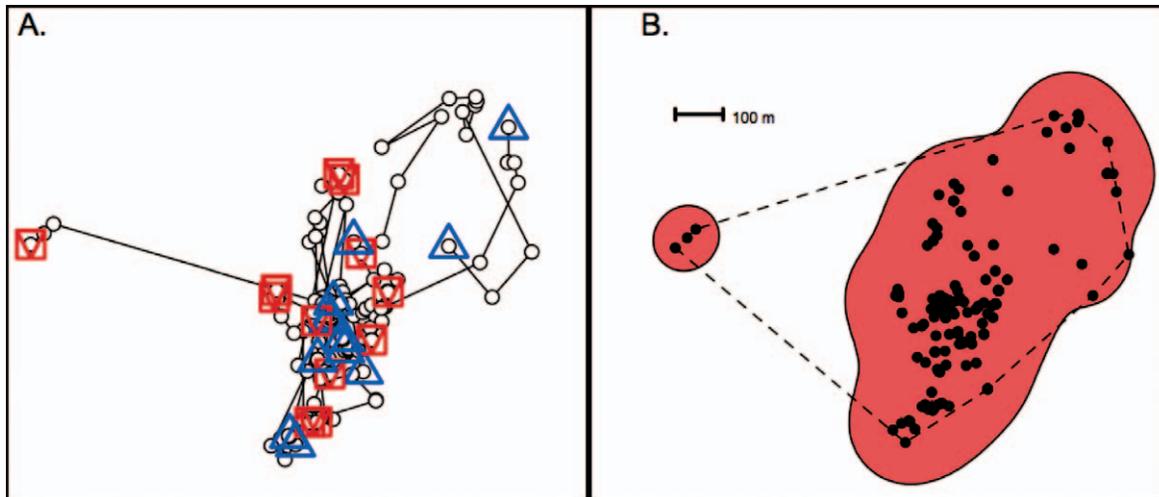


FIGURE 6. Illustration of radio telemetry data and basic home range for a single bird, W4. **(A)** Trajectories for each telemetry bout for W4. Each bout (12 total) consists of fixes (open circles) connected by a black line, extending from the first fix in a bout (blue triangle) to the last fix in a bout (red triangles inscribed in squares). **(B)** Traditional home-range estimators applied to telemetry data for W4. The 100% minimum convex polygon (MCP) home range is delineated by a dotted line. The 95% fixed kernel home range (using the “*h_{ref}*” method; Worton 1989) is colored red. Scale bar applies to both plots.

time between GPS points was not recorded. Instead, start times (t_0) and end times (t_1) for observed foraging bouts as well as elapsed time (E_x) at each location ($x = 1 \dots n$) were recorded. Distances traveled between consecutive fixes (d_x) were measured directly from tracking data. To estimate time intervals (I_x) between successively used foraging locations in 2011, we used the following equation:

$$I_x = \frac{(t_1 - t_0) - \sum_{x=1}^n E_x}{n - 1} \cdot \frac{d_x}{\sum_{x=1}^{n-1} d_x}$$

This equation divides the differences in bout start and end times minus the cumulative elapsed foraging time among all time intervals, proportional to the distance traveled between each pair of consecutive points. This assumes that birds traveled at a constant speed when traveling between foraging locations. Given that birds typically flew directly from one foraging tree to another, we consider this assumption valid.

While fixed-kernel methods require specification of only 1 variable related to kernel smoothing (i.e. spread; Worton 1989), parameterization of Brownian bridge kernel home ranges requires the specification of 2 variables. The first of these variables, sig1, is related to the speed of the animal and defines the width of Brownian bridges (Horne et al.

2007a). The second variable, sig2, is related to the imprecision of the relocations and defines the width of kernels around known locations. The parameter sig1 can be empirically estimated using data for a single bout (Horne et al. 2007a), but given that sig1 has meaning as a bird-specific rather than bout-specific property, we averaged empirical estimates of sig1 across all bouts for a single bird and used this single mean sig1 value for home-range estimation with all bouts of an individual. The parameter sig2 was set to 5 (m) for all birds, consistent with the average uncertainty of field-based GPS units used in our study.

Brownian bridge kernel estimation works best when the time between consecutive locations is relatively constant; thus, lumping bouts collected across multiple days or weeks into a single continuous movement trajectory invalidates model assumptions. To illustrate, if a second bout, tracked 2 wk after a first, started only 100 m from where the first ended, the uncertainty of where the individual bird could have gone during those 2 wk would be too great to fit a Brownian bridge. To avoid this problem, following Calenge (2009), we modeled kernel-based UD for individual observation bouts and then averaged all bout-specific UD (per individual) weighted by the number of fixes used to model each bout (Appendix B, Figure 7). This process creates a composite UD for an entire bird's home range.

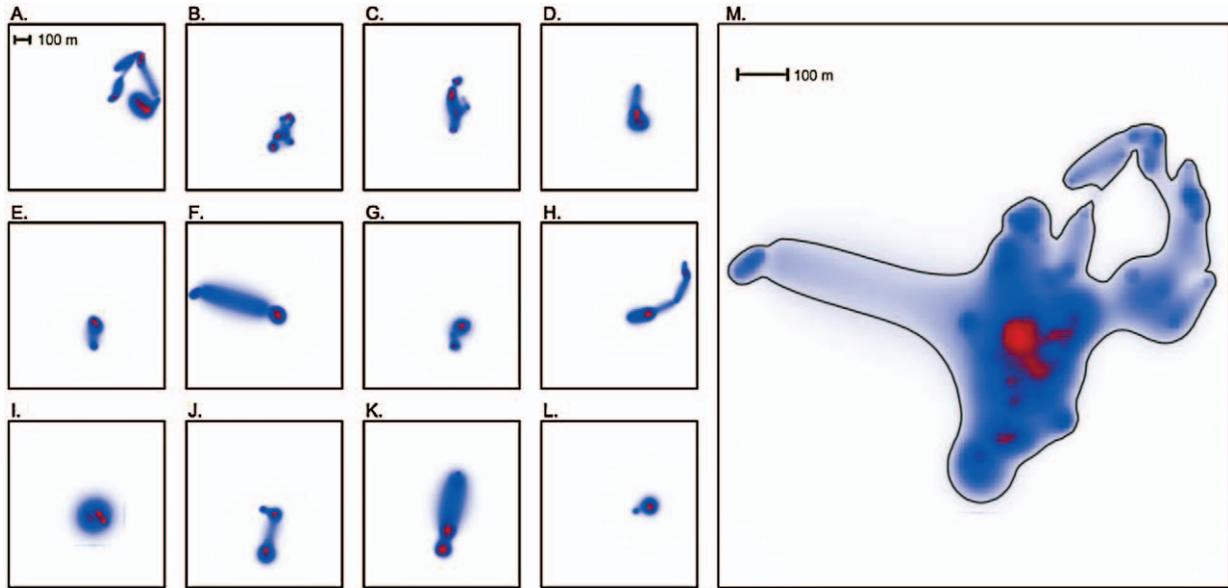


FIGURE 7. (A–L) By-bout Brownian bridge utilization distributions (UDs) for a single bird, W4, and (M) final weighted average home range. The UD_s are modeled for each bout separately in A–L, using constant individual-specific parameterizations and grids. The UD_s for all bouts are then averaged together, weighted by the number of fixes per bout (M). The UD_s are depicted in all plots as a gradient from white to blue to red. The solid line in M depicts the 95th percentile isopleth. The resulting home range (M) more truthfully models the observed animal trajectories (Appendix B, Figure 6, panel A) than using a fixed-kernel methodology (Appendix B, Figure 6, panel B). Scale for plot A held constant for plots B–L.