J. Field Ornithol. 92(3):273–283, 2021 DOI: 10.1111/jofo.12371

Nestling provisioning behavior of Black-backed Woodpeckers in post-fire forest

John K. Loverin,[1] Andrew N. Stillman,[1,5] Rodney B. Siegel,[2]
Robert L. Wilkerson,[2] Matthew Johnson,[3] and Morgan W. Tingley[4]

[1]*Ecology & Evolutionary Biology, University of Connecticut, 75 North Eagleville Road, Unit 3043, Storrs, Connecticut 06269, USA*
[2]*The Institute for Bird Populations, P.O. Box 518, Petaluma, California 94953, USA*
[3]*U.S. National Park Service, Southern Colorado Plateau Network – Inventory & Monitoring Division, 2255 North Gemini Drive, Flagstaff, Arizona 86001, USA*
[4]*Ecology and Evolutionary Biology, University of California – Los Angeles, 621 Charles E. Young Drive S #951606, Los Angeles, California 90095, USA*

Received 26 January 2021; accepted 2 June 2021

ABSTRACT. Provisioning behavior can have cascading effects on nest survival, juvenile recruitment, and parental fitness. Provisioning behavior may be influenced by temporal variables, such as nestling age, or habitat variables, such as food availability and landscape disturbance. Black-backed Woodpeckers (*Picoides arcticus*) are associated with burned forests, where they nest in stands of fire-killed trees. Our objectives were to determine if their nestling provisioning behavior is influenced by the characteristics of fires and post-fire management, and if provisioning behavior differs with sex and varies across the breeding season. We recorded provisioning rates and the size of prey deliveries at 21 nests of Black-backed Woodpeckers in a burned area of northern California in 2014–2015 and examined the possible effects of habitat, temporal variables, and parental sex on provisioning rates and prey delivery size using mixed-effects models. Provisioning rates were higher for early season nests than late-season nests, and provisioning rates increased with nestling age. The size of prey provided to nestlings increased with nestling age, and prey delivery size was also larger for nests near areas where post-fire logging had occurred. Parental sex had no effect on either provisioning rates or prey delivery size. Our results suggest that, in burned forests in our study area, Black-backed Woodpeckers provisioning nestlings respond more strongly to temporal variables than habitat variables, and both sexes contribute equally to feeding young. Temporal variation in provisioning rates and prey delivery size likely reflect variation in the energetic demands of nestlings.

RESUMEN. **Comportamiento de aprovisionamiento de pichones en *Picoides arcticus* en el bosque posterior al incendio**

El comportamiento de aprovisionamiento puede tener un efecto cascada sobre la supervivencia de los nidos, reclutamiento de los juveniles y aptitud de los parentales. El comportamiento de aprovisionamiento puede estar influenciado por variables temporales, como la edad de los pichones, o variables del hábitat, como la disponibilidad de alimento y el disturbio en el paisaje. *Picoides arcticus* están asociados a bosques propensos a incendios, donde los nidos son ubicados en arboles afectados por el fuego. Nuestros objetivos fueron los de determinar si el comportamiento de aprovisionamiento de los pichones esta influenciado por las características de los incendios y el manejo posterior al incendio, y si el comportamiento de aprovisionamiento difiere con el sexo y varia a través de la temporada de reproducción. Colectamos información sobre tasas de aprovisionamiento y el tamaño de las presas entregadas en 21 nidos de *Picoides arcticus* en un área incendiada del norte de California en 2014–2015 y examinamos los posibles efectos del hábitat, las variables temporales y el comportamiento parental de cada sexo sobre las tasas de aprovisionamiento y el tamaño de las presas entregadas usando modelos de efectos mixtos. Las tasas de aprovisionamiento fueron mayores para nidos construidos temprano en la temporada que en nidos construidos tarde en la temporada, y las tasas de aprovisionamiento incrementaron con la edad de los pichones. El tamaño de la presa entregado a los pichones incrementó con la edad de los pichones, y el tamaño de la presa entregada también fue mayor para nidos cerca de áreas donde existió tala posterior al incendio. Nuestro resultados sugieren que en bosques incendiados, en nuestra área de estudio, el aprovisionamiento de pichones en *Picoides arcticus* responde más fuertemente a variables temporales que a variables de hábitat, y que ambos sexos contribuyen igualmente a la alimentación de los polluelos. La variación temporal en tasas de aprovisionamiento y el tamaño de presa entregada posiblemente refleja la variación en las demandas energéticas de los pichones.

Key words: foraging, logging, nest, parental investment, *Picoides arcticus*, wildfire

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[5] Corresponding author. Email: stillman.andrewn@gmail.com

A key component of parental investment is the need to provision altricial young. When provisioning nestlings, parents incur additional exposure to predators and pathogens (Mutzel et al. 2013), as well as energetic costs associated with flight, search, and prey capture (Nur 1984). Provisioning rates may also respond to environmental variation, with cascading effects on population parameters such as nestling survival and juvenile recruitment (Bortolotti et al. 2011). Thus, information about provisioning behavior can be useful when assessing habitat quality, possible impacts of landscape change, and other potential threats species may experience in breeding areas (Amar et al. 2003, Tremblay et al. 2005, Mennechez and Clergeau 2006).

Black-backed Woodpeckers (*Picoides arcticus*) are associated with snag forest habitat, where they breed in dense stands of dead trees that provide nesting and foraging substrates (Tremblay et al. 2015, Stillman et al. 2019a). In the western United States, these woodpeckers are most often observed in areas after recent stand-replacing fires (Hutto 2008). Elsewhere in their range, Black-backed Woodpeckers are found in other forest types with available snags such as old coniferous forests or forests with recent insect disturbances (Tremblay et al. 2009, Rota et al. 2015). These woodpeckers forage primarily on arthropods associated with dead wood, particularly the larvae of woodboring beetles that thrive in dead and dying trees after a fire (Beal 1911, Murphy and Lehnhausen 1998), and they show strong selection for dead trees when excavating nest cavities (Nappi and Drapeau 2011, Stillman et al. 2019a). In post-fire areas of the western United States, nest densities typically peak 4–5 years following a fire, after which availability of beetle prey typically declines (Tingley et al. 2018, Ray et al. 2019).

Previous studies of provisioning behavior of Black-backed Woodpeckers have revealed temporal patterns and differences between the sexes. For example, female Black-backed Woodpeckers may make fewer provisioning trips near the end of the nestling period, sometimes even ceasing provisioning altogether (Winkler and Short 1978). However, some investigators have found that females provision nestlings more frequently than males (Kilham 1966, Short 1974), whereas others have reported no differences between the sexes (Tremblay et al. 2016). In boreal forests in Quebec, provisioning rates of Black-backed Woodpeckers were lower in unburned than in burned forests, reflecting the need for greater foraging effort in unburned areas and potential negative effects on nestling survival (Tremblay et al. 2016). Woodpeckers also capture larger prey when foraging in burned forests than in other types of disturbed forests (Rota et al. 2015). Possibly because of these factors, Black-backed Woodpeckers are more than 12 times more abundant in burned forests than in nearby beetle-killed forests in California, USA (Tingley et al. 2020). However, preferred stands of burned forest are frequently subject to post-fire logging that can render the habitat less suitable and reduce nest densities accordingly (Saab et al. 2007). Despite these threats to breeding habitat, little is known about the provisioning behavior of Black-backed Woodpeckers in burned forests or how provisioning behavior might be influenced by differences in the characteristics of fires and post-fire management.

Provisioning behavior is often affected by a combination of habitat and temporal factors. For example, Blue Tits (*Cyanistes caeruleus*) nesting in poor habitat had lower provisioning rates due to longer foraging bouts (Tremblay et al. 2005), and birds foraging in areas with lower prey densities may have longer search times and reduced survival overall (Thomas et al. 2001). Changes in provisioning behavior due to habitat quality may influence bird population trends, particularly for species like Black-backed Woodpeckers that are associated with particular resource types. In addition, temporal factors such as the age of nestlings or time of year can influence provisioning behaviors. For altricial species, provisioning rates may increase with nestling age and then plateau before nestlings fledge (Nice 1937). This pattern has been demonstrated in Tree Swallows (*Tachycineta bicolor*), where provisioning rates increase with nestling age for the first 10 days and then level off (Leffelaar and Robertson 1986). In non-passerines, Wiktander et al. (2000) found that the provisioning rates of Lesser Spotted Woodpeckers (*Dryobates minor*) increased from 8.8 to 13.6 deliveries per hour from the early to late nestling stage. This increase in provisioning rate with nestling age is likely due to the increased energy demands of nestlings as they age (Goodbred and Holmes 1996). Provisioning rates may also show temporal trends independent of the nestling stage due to seasonal variation in food availability, predation risk, or the quality of breeding individuals (Perrins 1970, Arnold et al. 2004).

In many woodpecker species, males provide as much or more parental care than females (Wiebe 2008). In particular, males may incubate eggs, brood young at night, and perform most of the nest sanitation duties (Wozniak and Mazgajski 2003, Tremblay et al. 2016). In some species, males provision young more (Gow et al. 2013) or deliver larger prey than females (Chazarreta et al. 2011). This relatively high investment by males may be the result of high male assurance of paternity in woodpeckers (Gow et al. 2013). However, many investigators have reported no differences in the provisioning rates of male and female woodpeckers (Wiebe and Elchuk 2003, Woźniak and Mazgajski 2003, Kozma and Kroll 2013).

We observed nests of Black-backed Woodpeckers in a burned forest to examine the possible influence of temporal variables, habitat variables, and parental sex on provisioning behavior. Specifically, we examined nestling provisioning rates and the size of prey delivered to the young. Forest stands that burn severely with high tree mortality provide high food densities (Ray et al. 2019), which may reduce the time woodpeckers spend searching for food and traveling between foraging locations. Thus, we hypothesized that provisioning behavior would respond to habitat characteristics such as burn severity, as well as management actions such as post-fire logging that remove foraging substrates (snags) from the landscape. In addition, we predicted that provisioning behavior would respond to several temporal factors. We expected that parents would increase provisioning rates and the size of prey deliveries with increasing nestling age, and that adults at nests initiated earlier in the season, with potentially more experience, would have higher provisioning rates. Lastly, because of the high assurance of paternity in woodpeckers and male involvement in nestling care, we predicted that male and female Black-backed Woodpeckers would provision nestlings at similar rates. Black-backed Woodpeckers are frequently used as a management indicator species in burned forests, and our study provides important information about factors that might influence provisioning behavior in these areas.

METHODS

We observed Black-backed Woodpecker nests in the area burned by the Moonlight Fire in Plumas County, California, U.S.A. In September 2007, the Moonlight Fire burned ~ 263 km^2 of mixed-conifer forest in the Sierra Nevada mountain range, a forest dominated by *Pinus ponderosa*, *P. jeffreyi*, *P. lambertiana*, *Calocedrus decurrens*, *Abies concolor*, and *Pseudotsuga menziesii*. In the burned area, 47% was classified as high severity, with $\geq$ 95% reduction in canopy cover after the fire (RAVG: https://fsapps.nwcg.gov/ravg/). All of our nest observations occurred in 2014 and 2015, or 7–8 years after the fire. Although populations of Black-backed Woodpeckers in burned forests in this region generally decline starting around five years after fires (Tingley et al. 2018), breeding pairs were still present at moderate densities during our study (Stillman et al. 2019a). Our study was conducted on portions of public land that had not been subject to clear-cut post-fire logging, but some of the study area was adjacent to private lands that had been logged within two years after the fire. Previous work has shown that nesting Black-backed Woodpeckers generally avoid areas with extensive post-fire logging, particularly when private holdings are clear-cut and replanted with conifers (Tarbill et al. 2018).

Field methods. We located breeding pairs primarily using broadcast surveys from mid-April to late July during both years of our study. We attempted to cover most of the area by surveying a 500-m grid of points arrayed throughout the burned area. In addition, we conducted ad hoc surveys along Forest Service roads. During surveys, we broadcast woodpecker vocalizations and sounds of territorial drumming. When a woodpecker responded, we followed it to locate a nest and sometimes revisited the site multiple days while searching.

We attempted to visit nests every 2–5 days (mean interval = 3 days) to determine nest stage and collect behavioral data. After eggs hatched (determined based on changes in parental behavior because we were not able to see into most nests), we recorded provisioning behavior during each monitoring visit using either 30- or 60-min observation periods, depending on field crew constraints. When woodpeckers brought prey to nests, we recorded the size of prey deliveries relative to the bill and categorized sizes as small (< 0.5× length of the bill), medium (≥ 0.5× and ≤ 1× length of the bill), or large (> 1× length of the bill) and noted the sex of the bird. We observed delivery sizes using both binoculars and a spotting scope, and deliveries could constitute one or more individual prey items carried during a single provisioning visit. For 30-min observation periods ($N = 18$ of 67 total), we calculated hourly provisioning rates by doubling the number of observed prey deliveries. Although a single provisioning event could include multiple prey items in a single delivery, our observations indicated that parents almost always delivered one visible prey item at a time. However, our method of measuring delivery size relative to bill size did not assume that each provisioning event represented a single prey item. To determine nest-initiation dates, we subtracted 40 days from the date that nestlings fledged, using published estimates of the duration of the nesting period for Black-backed Woodpeckers (Tremblay et al. 2020). As estimated fledging dates approached, we increased the frequency of nest visits (every 1–2 days) to more accurately record those dates.

Habitat variables. We used remotely sensed data to measure habitat variables with potential effects on provisioning behavior. We calculated the average burn severity within 500 m of each nest, measured as the percent change in canopy cover from before to immediately after fire, using Landsat-derived burn severity layers created by the Rapid Assessment of Vegetation Condition after Wildfire program (https://fsapps.nwcg.gov/ravg/). We also calculated the distance of each nest from the nearest area (i.e., 30 × 30-m pixel) that burned at low severity or remained unburned, with low severity defined as a change in canopy cover ≤ 4.4%. The 4.4% threshold represents the median value of points classified as low severity based on a field survey of ~ 10,000 burned survey points (Stillman et al. 2019b). Finally, we used Google Earth satellite imagery from 2007 to 2014, combined with land-ownership data, to map areas that were clear-cut logged after the fire. We used this spatial layer to calculate the proportion of burned area within 500 m of each nest subject to post-fire logging.

Statistical analysis. To characterize parental behavior, we used the (1) number of times males and females delivered prey per hour (provisioning rate) and (2) relative size of prey deliveries. We used generalized linear mixed-effects models with a negative binomial error distribution to determine the factors that influenced provisioning rates. Random intercepts were used for each nest due to the non-independence of repeated observations over time. In these models, we calculated a separate provisioning rate for each observation period at each nest. We built a candidate model set based on *a priori* hypotheses about the temporal and habitat variables that may influence provisioning rate (Table S1). First, we tested whether nestling age fit better as a linear or quadratic variable. We found that including nestling age as a quadratic effect performed best so we used this variable in subsequent candidate models. To prevent model overfitting, we limited each candidate model to a maximum of three predictor variables. We compared candidate models in an information-theoretic framework using $\mathrm{AIC_c}$ and used AIC weights and cumulative weights for multi-model inference (Burnham and Anderson 2002). We also performed an unpaired t-test to determine if one sex had a higher provisioning rate. For this test, we calculated a single provisioning rate across all observation periods for each sex at each nest.

We used mixed-effects ordinal regression models (also called cumulative link mixed models) to test factors that influence prey delivery size (Guisan and Harrell 2000). As measured in the field, our response variable was the number of prey deliveries made per sex per observation period in each prey delivery size category. Similar to our provisioning rate models, we used $\mathrm{AIC_c}$ to compare linear and quadratic forms of nestling age and determined that the linear version performed best. The candidate model set consisted of the same combinations of variables used in models of provisioning rate, which we compared using $\mathrm{AIC_c}$ and used AIC weights and cumulative weights for multi-model inference (Burnham and Anderson 2002). Additionally, we used a chi-square test to evaluate the independence of prey delivery size and sex.

Both sets of models were checked for appropriate fit. For the top model of prey delivery size, we used a likelihood ratio test to assess relative model fit compared to an intercept-only model and confirmed that the model satisfied the proportional odds assumption. Similarly, we evaluated the top model of provisioning rate by comparing it against a null model using parametric bootstrapping with the R package "pbkrtest" (Halekoh and Højsgaard 2014). We also computed a conditional (accounts for both random and fixed effects) and marginal (accounts for just fixed effects) R^2 value for the top provisioning rate model (Nakagawa and Schielzeth 2013, Lüdecke et al. 2020). All analyses were completed in the program R version 3.5.1 using the packages lme4 (Bates et al. 2014), MASS (Venables and Ripley 2002), and ordinal (R Core Team 2018, Christensen 2019). Values are presented as means ± 1 SD.

RESULTS

We analyzed data collected during 67 observation periods at 21 nests, resulting in 58 hours of nest observations and an average of 2.8 ± 1.9 observation hours per nest. We recorded 233 nest visits by females and 254 nest visits by males. Of 487 observations, prey were delivered during 380 nest visits, and we determined the relative size of prey deliveries in 306 cases (89 small, 159 medium, and 58 large). The mean ordinal date of nest initiation was 116 ± 12 (~ 25 April), with a range from 99 to 149 (8 April – 28 May). Overall, the mean provisioning rate was 6.5 ± 4.0 deliveries per hour (range = 0–20), with mean rates of 3.5 ± 1.7 deliveries per hour for males and 3.0 ± 1.6 deliveries per hour for females. Monitored nests were in areas that primarily burned at high severity, with an average post-fire reduction in canopy cover within 500 m of nests of 74.3 ± 23.4%. The mean distance between nests and the closest area either burned at low severity or left unburned was 365 ± 388 m. Within a 500-m buffer around nests, the average proportion of forest subject to post-fire logging was 12.0 ± 17.8% (range = 0–59.9%).

The top model for provisioning rate received strong support (AIC_c weight = 0.78; Table 1) relative to other candidate models and included a quadratic effect of nestling age (cumulative AIC_c weight = 1) and a linear effect of nest-initiation date (cumulative AIC_c weight = 0.78). Predictions from the top model showed a peak in provisioning rate when nestlings were 16 days old, or ~ 9 days before fledging (Fig. 1A). Provisioning rates were higher at nests initiated earlier in the season than those initiated later in the season (Fig. 1B, Table 2). Provisioning rates of males and females did not differ ($t_{39.96} = -1.2$, $P = 0.25$). The top model of provisioning rate had a conditional R^2 of

Table 1. Model comparisons for the set of 11 candidate models of provisioning rates of Black-backed Woodpeckers in the Moonlight fire, California. Provisioning rate (number of prey deliveries/hour) was calculated separately for each observation period at each nest. Models are shown in order of ascending AIC_c values, where ΔAIC_c is equal to the difference in AIC_c from the top model.

Model[a]	K[b]	AIC_c	ΔAIC_c	AIC weight
Nestling Age + Nestling Age^2 + Initiation[c]	5	353.14	0.00	0.78
Nestling Age + Nestling Age^2	4	356.65	3.51	0.13
Nestling Age + Nestling Age^2 + Logging	5	357.51	4.37	0.09
Initiation	3	368.55	15.41	0
Logging	3	368.99	15.85	0
Initiation + Logging	4	369.13	15.99	0
Burn severity + Logging	4	369.49	16.35	0
Intercept only	2	370.09	16.95	0
Burn severity	3	370.44	17.30	0
Dist. to low + Logging	4	371.30	18.16	0
Logging + Burn severity + Dist. to low	5	371.35	18.21	0
Dist. to low	3	372.00	18.86	0

[a] All models included random intercepts for nest.

[b] Number of parameters.

[c] Initiation refers to the calculated or observed date that the first egg was laid.

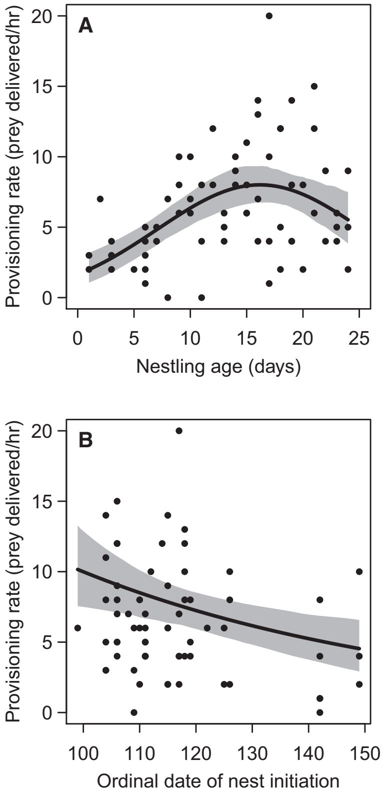

Fig. 1. Modeled relationships for the top model for provisioning rates of Black-backed Woodpeckers, which included effects of (A) nestling age and (B) ordinal nest-initiation date.

Table 2. Coefficients estimates for top models of Black-backed Woodpecker parental behavior as measured by provisioning rate and size of prey delivered. Estimates show means and 95% confidence intervals for parameters in the top model.

Model	Parameter estimate
Provisioning rate	
Intercept	2.04 (1.88, 2.19)
Nestling age	0.20 (0.06, 0.34)
Nestling age^2	−0.25 (−0.40, −0.13)
Initiation	−0.20 (−0.34, −0.07)
Prey delivery size	
Nestling age	0.29 (0.03, 0.54)
Logging	0.44 (0.03, 0.86)

Table 3. Model comparisons for the set of 11 candidate models for the size of prey delivered by Black-backed Woodpeckers. Prey delivery sizes were categorized as small, medium, or large. Models are shown in order of ascending AIC_c values, where ΔAIC_c is equal to the difference in AIC_c from the top model.

Model[a]	K[b]	AIC_c	ΔAIC_c	AIC Weight
Nestling age + Logging	4	598.09	0.00	0.41
Nestling age	3	600.13	2.04	0.15
Logging + Burn severity + Dist. to low	5	601.04	2.95	0.09
Logging	3	601.10	3.01	0.09
Nestling Age + Initiation[c]	4	602.07	3.98	0.06
Burn severity + Logging	4	602.33	4.24	0.05
Dist. to low + Logging	4	602.45	4.36	0.05
Initiation + Logging	4	603.10	5.01	0.03
Intercept only	2	603.21	5.12	0.03
Dist. to low	3	603.63	5.54	0.03
Burn severity	3	604.69	6.60	0.01
Initiation	3	605.04	6.95	0.01

[a] All models included random intercepts for nest.
[b] Number of parameters.
[c] Initiation refers to the calculated or observed date that the first egg was laid.

0.40 and a marginal R^2 of 0.38. Model evaluation indicated that variables in the top model explained a significant amount of deviance and the top model provided a better fit than the null model (parametric bootstrapping test, $P = 0.015$).

The size of prey deliveries also did not differ by sex ($\chi^2_2 = 4.4$, $P = 0.11$). Our multimodel approach indicated important linear effects of nestling age (cumulative AIC_c weight = 0.62) and post-fire logging (cumulative AIC_c weight = 0.72) on the size of prey deliveries. The best-supported model (AIC_c weight = 0.41) included both of these variables (Table 3). The size of prey deliveries increased linearly with increasing nestling age, with a 5-day increase in nestling age increasing the likelihood of a parent bringing a large prey item (versus medium and small) by a factor of 1.3. The probability of a large prey delivery also increased with the proportion of post-fire logging within 500 m of nests (Fig. 2, Table 2). A likelihood ratio test

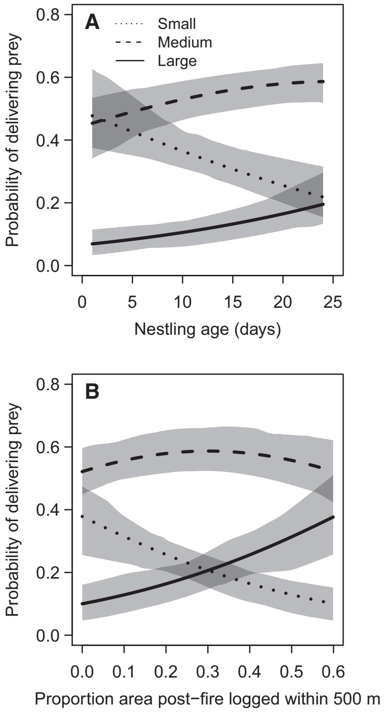

Fig. 2. Modeled relationships for the top model of prey delivery size for adult Black-backed Woodpeckers, measured as the probability of bringing small, medium, or large prey deliveries. The top model included (A) effects of nestling age, and (B) area within 500 m of nests logged after fire.

showed that both variables significantly improved model fit compared to an intercept-only model ($P = 0.01$), and we confirmed that the model satisfied the proportional odds assumption (Guisan and Harrell 2000).

DISCUSSION

Overall, we found that temporal variables had a greater effect on the provisioning behavior of Black-backed Woodpeckers than the measured habitat variables. The top model for provisioning rate included a hump-shaped effect of nestling age, with provisioning rates peaking when nestlings were 16 days old and a linearly decreasing effect of nest-initiation date. Based on ordinal regression model estimates, the size of prey deliveries increased with nestling age and with the amount of post-fire logging near nests. Contrary to our hypothesis that Black-backed Woodpeckers would provision at higher rates and deliver larger prey in severely burned areas, our models revealed no relationship between provisioning behavior and this habitat characteristic. However, all nests in our dataset were in patches of relatively high-severity burn. Therefore, variation in our measured habitat covariates may not have been sufficient to reveal an effect of burn severity, as previously described for Black-backed Woodpeckers (Tremblay et al. 2016). These woodpeckers likely seek out high-quality habitats for nesting and foraging, which can limit detection of habitat-based effects (Stillman et al. 2019a). The absence of habitat-based variation in provisioning behavior supports the idea that Black-backed Woodpeckers are habitat specialists that select severely burned patches for nesting in the western U.S.

We found that nestling age strongly affected provisioning behavior, with provisioning rates peaking around 16 days post-hatching and shifts to larger prey deliveries as nestlings aged. Generally, increased provisioning rates during the early nestling period are due to increasing energy demands of the young (Goodbred and Holmes 1996). We did not predict that provisioning rates would peak well before nestlings fledged, but this has been reported in previous studies. For example, Leffelaar and Robertson (1986) found that provisioning rates of Tree Swallows increased for the first 10 days before leveling off until fledging. Growth rates of nestling Black-backed Woodpeckers plateau around 11–14 days post-hatching (Tremblay et al. 2014). In addition, adults may reduce the amount of prey delivered to nestlings prior to fledging to encourage the young to leave nests (Wiebe and Elchuk 2003). Provisioning rates may also plateau or decline late in the nestling period because parents bring larger or more prey per visit, which could reduce the costs associated with frequent travel between the nest and favored foraging areas. Rytkönen et al. (1996) found that the size of prey brought to nestlings by adult Willow Tits (*Poecile montanus*) increased during the breeding season. A combination of increasing provisioning rates and prey delivery sizes may allow parents to compensate for variation in the energy demands of nestlings.

Nest-initiation date was negatively correlated with provisioning rate, but it did not affect prey delivery size. Birds that nest later in the season may be in poorer condition or have less parental experience, leading to lower provisioning rates (Perrins 1970, Arnold et al. 2004). Late-nesting birds may also have reduced nest success, as shown previously for Black-backed Woodpeckers, Hairy Woodpeckers (*Dryobates villosus*), and Northern Flickers (*Colaptes auratus*, Kozma and Kroll 2012, Stillman et al. 2019a). Woodpeckers that initiated nesting later in the season may have been delayed due to inexperience with cavity-site selection and excavation (Kozma and Kroll 2012) or could be attempting to nest a second time after a first attempt failed. Pechacek (2006) found that females paired with more experienced males laid eggs earlier in the season, suggesting that nest initiation may be linked with provisioning rate and that provisioning rate may serve as an indicator for the likelihood of nest survival. Woodboring beetle larvae, the main prey of Black-backed Woodpeckers in burned habitats, can live inside dead and dying trees for multiple years before emerging and are available year-round in our study region. Thus, the relationship between initiation date and provisioning behavior likely does not reflect seasonal changes in either prey availability or size.

Pairs with nests near areas with more post-fire logging provisioned young with larger prey deliveries. These same nest conditions also showed a weak negative effect on provisioning rate ($P = 0.051$), although the extent of post-fire logging was not in the top model for provisioning rate. A negative effect of increased logging on provisioning rate was expected because snag removal may force woodpeckers to travel farther between foraging sites (Murphy and Lehnhausen 1998). However, we did not expect Black-backed Woodpeckers to bring larger deliveries to nests where post-fire logging was more prevalent, so this result deserves further study. Larger prey deliveries could result if woodpeckers compensate for the increased duration of provisioning trips by providing nestlings with more food per trip. In general, Black-backed Woodpeckers provisioning young select prey items that average larger than available prey (Powell 2000). In addition, Stephens and Krebs (1986) suggested that parents tend to bring larger prey deliveries when foraging patches are farther away. Similarly, Tremblay et al. (2005) found that Blue Tits were able to offset a drop in provisioning rate due to poor habitat surrounding nests by providing young with 73% larger prey. This matches what we observed in our study, although more data are needed to better understand the relationship between post-fire logging and provisioning rates.

We found no effect of sex on either provisioning rates or prey delivery size, which is consistent with our prediction of similar contributions by male and female woodpeckers when provisioning young. Similar results have been reported in previous studies of woodpeckers, many of which revealed no differences in provisioning rates of males and females (Wiebe and Elchuk 2003, Woźniak and Mazgajski 2003, Kozma and Kroll 2013). However, parental effort in a broader context may differ between the sexes, and previous research has shown that male Black-backed Woodpeckers perform more nest sanitation and incubation (Short 1982, Tremblay et al. 2016). Therefore, males of this species may still have higher overall parental effort even if provisioning rates are equal.

One potential area for future study is to examine the possible effect of brood size on provisioning rates. We were unable to access nestlings because nests were too high above ground in unstable, dead trees. Tremblay et al. (2016) found that Black-backed Woodpeckers with three young provisioned at higher rates than those with two. In a separate study of Black-backed Woodpecker nesting biology in the Moonlight and other fires in California, 10 of 23 nests had two nestlings, 11 had three, and one had four (A. N. Stillman, unpubl. data). Nest-initiation date may also be correlated with the number of nestlings. In some species, lower-quality parents have smaller broods (Sydeman et al. 1991) and tend to nest later in the breeding season (Koenig and Walters 2018). Thus, higher provisioning rates earlier in the season could be due to the presence of a greater number of nestlings. Additional observations in other burned areas for longer periods could help determine if nest success and time since fire are influenced by provisioning rates and prey delivery size. We had insufficient variation in nest success and time since fire to examine those relationships, but speculate that time since fire (i.e., 1–10 years post-fire) may have a positive relationship with provisioning rate and a negative relationship with prey delivery size, which in turn could affect nest success in burned forests. This is because decreasing abundance of woodboring beetles with time since fire may reduce availability of large prey items and force parents to compensate by making more frequent foraging trips.

More broadly, our results suggest that habitat variables may have less influence than temporal variables on the provisioning behavior of Black-backed Woodpeckers nesting in burned areas. Because provisioning behaviors can act as an index of parental effort (Siegel et al. 1999), it is important to determine how provisioning changes over the course of the nestling period. Understanding these behaviors may then increase our understanding of the mechanisms leading to variation in nest success, juvenile recruitment, and adult fecundity in birds (Bortolotti et al. 2011).

ACKNOWLEDGMENTS

This project was funded by Plumas National Forest. We thank Angela Haas, Anna Frujoff-Hung, Caitlin Miller, Cary Fly, Frankie Tousley, Jenna Hooper, Katie McLaughlin, Kristen Heath, and Niles Desmarais for collecting nest provisioning data and Matt Lerow for providing field supervision. This research was conducted in adherence to the Ornithological Council's Guidelines to the Use of Wild Birds in Research (Fair et al. 2010). Drafts of this manuscript benefitted from feedback by Robert Bagchi and three anonymous reviewers. This is Contribution No. 684 of The Institute for Bird Populations.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's website.

Table S1. Candidate model set for woodpecker provisioning rate and prey delivery size based on *a priori* hypotheses about the temporal and habitat variables that may influence provisioning behavior.