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Research Paper

Snag density and stand age, but not stand size, explain occupancy and reproduction of an imperiled cavity nester in early successional forest

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ABSTRACT. Many early successional and disturbance-dependent bird species have declined over the past several decades. Cavity-nesting birds in early successional forests are vulnerable because they often require specific habitat characteristics and frequent disturbance events. We examined whether stand age (a proxy for forest succession), stand size, and snag density explained occupancy, nest survival, and productivity of a threatened cavity nester, the Southeastern American Kestrel (*Falco sparverius paulus*), in natural cavities in early successional forest (≤ 15 years since treatment). We conducted point counts, nest searching, and monitoring during the 2018–2019 breeding seasons in sand pine (*Pinus clausa*) scrub habitat in Ocala National Forest, Florida. Stands were created by either a clearcut, a clearcut followed by prescribed burn, or wildfire. Occupancy probability tended to peak in stands ≤ 5 years old, but this varied with snag density: $\beta_{\text{standage} \times \text{snagdensity}} = -1.40$, 95% CI (-2.57, -0.23). Even slight increases in snag density were related to large increases in occupancy across stand ages. For example, our occupancy model predicted that if there were 5 snags/ha, there was a 70% probability of occurrence (per point) in a four-year-old stand, whereas 1 snag/ha led to expected occupancy probability of 30%. Nest survival was best explained by snag density: $\beta_{\text{snagdensity}} = 0.71$, 95% CI (0.12, 1.46). Neither occupancy nor nest survival were explained by stand size. Productivity did not have a relationship with any measured covariate. Our data indicate that snag density is an important measure of habitat quality for cavity-nesting birds and that interpreting stand age without considering the role of snag density may lead to under- or overestimating habitat quality of stands. Occupancy probability and nest survival had a low positive correlation across clearcut stands, but not in prescribed burns or wildfires. These results emphasize caution when extrapolating predictions from clearcuts to wildfire or prescribed burn stands.

La densité de chicots et l'âge du peuplement, mais pas la taille du peuplement, expliquent l'occupation et la reproduction d'un nicheur cavicole menacé en forêt de début de succession

RÉSUMÉ. De nombreuses espèces d'oiseaux de début de succession et dépendant des perturbations ont diminué au cours des dernières décennies. Les oiseaux qui nichent dans des cavités en forêt de début de succession sont vulnérables, car ils recherchent souvent des caractéristiques d'habitat spécifiques, qui nécessitent des perturbations fréquentes. Nous avons examiné si l'âge du peuplement (un indicateur de succession forestière), la taille du peuplement et la densité de chicots expliquaient l'occupation, la survie des nids et la productivité d'un nicheur cavicole menacé, la Crécerelle d'Amérique du Sud-Est (*Falco sparverius paulus*), dans des cavités naturelles en forêt de début de succession (≤ 15 ans depuis le traitement). Nous avons effectué des dénombrements par points d'écoute, des recherches de nids et un suivi au cours des saisons de reproduction 2018-2019 dans un peuplement de jeunes pins des sables (*Pinus clausa*) dans la forêt nationale d'Ocala, en Floride. Les peuplements ont été créés soit par une coupe totale, soit par une coupe totale suivie d'un brûlage dirigé, soit par un feu de forêt. La probabilité d'occupation avait tendance à atteindre un pic dans les peuplements ≤ 5 ans, mais elle variait avec la densité de chicots : $\beta_{\text{âgedupeuplement} \times \text{densitédechicots}} = -1,40$, I.C. 95 % (-2,57, -0,23). Même de légères augmentations de la densité de chicots étaient liées à de fortes augmentations de l'occupation à travers les âges des peuplements. Par exemple, notre modèle d'occupation prédisait que s'il se trouvait 5 chicots/ha, la probabilité d'occurrence (par point) dans un peuplement de quatre ans était de 70 %, alors qu'une densité de 1 chicot/ha correspondait à une probabilité d'occupation de 30 %. La survie des nids était mieux expliquée par la densité de chicots : $\beta_{\text{densitédechicots}} = 0,71$, I.C. 95 % (0,12, 1,46). Ni l'occupation, ni la survie des nids, n'ont montré une relation avec la taille des peuplements. La productivité ne montrait pas de relation avec les covariables mesurées. Nos données indiquent que la densité de chicots est une mesure importante de la qualité de l'habitat pour les oiseaux cavicoles, et que l'interprétation de l'âge du peuplement, sans prendre en compte le rôle de la densité de chicots, peut conduire à une sous-estimation ou une surestimation de la qualité des peuplements en tant qu'habitat. La probabilité d'occupation et la survie des nids présentaient une faible corrélation positive dans les peuplements de coupe totale, mais aucune dans les brûlages dirigés ou les feux de forêt. Ces résultats incitent à la prudence dans le cas d'extrapolations des prédictions réalisées dans des coupes totales aux peuplements issus de feux ou de brûlages dirigés.

Key Words: *cavity-nesting birds; early successional forest; Falco sparverius paulus; habitat quality; nest survival; occupancy; sand pine scrub; snag density; stand age; stand size*

Erratum: In the original publication there was an error in Figure 5. A corrected version of the graph was added on 17 November 2022.

INTRODUCTION

Many early successional and disturbance-dependent bird species have declined since at least the 1950s (Brawn et al. 2001, Hunter et al. 2001, Rosenberg et al. 2019) because of habitat loss and suppression of natural disturbance events, e.g., fires and floods (Askins 2001). These changes can influence many aspects of habitat that have the potential to affect birds in early successional forests. For example, stand age reflects the potential stage of successional dynamics and the relevant habitat structure that animals may use (Schieck and Song 2006, Resasco and Fletcher 2021). In addition, stand size is often considered for management of early successional habitat because habitat loss and certain disturbance events, e.g., wind or construction of power-line corridors, can create relatively small openings and, as a consequence, potentially limit birds' ability to use the stands for breeding (Krementz and Christie 2000, Shake et al. 2012, King and Schlossberg 2014). However, the relationship between occupancy, reproduction (e.g., nest success, productivity), and stand size may be inconsistent. For example, although increasing stand size may increase occupancy probability (Shake et al. 2012) or abundance (Chandler et al. 2009), it may not be important for reproductive effort (Krementz and Christie 2000) or nest survival (King et al. 2001). Similarly, nest density may not be a good indicator of nest survival with increasing stand age (Saab et al. 2007).

Another important component of early successional habitat is snag density. Snag density varies with stand age and disturbance type (Cline et al. 1980, Moorman et al. 1999, Greenberg et al. 2018, Johnson et al. 2020). Cavity-nesting birds are often limited by snag availability (Raphael and White 1984, Kilgo and Vukovich 2014). Snag density is positively related to cavity-nester density (Land et al. 1989, Breininger and Smith 1992) and species diversity (Zarnowitz and Manuwal 1985) because it can alter the availability of nest sites (Saab et al. 2009, Stillman et al. 2019). Snag excavation by primary cavity nesters, e.g., Hairy Woodpecker (*Leuconotopicus villosus*) and Northern Flicker (*Colaptes auratus*), creates opportunities for use by secondary cavity nesters (Trzcinski et al. 2021), e.g., Eastern Screech-Owl (*Megascops asio*) and Eastern Bluebird (*Sialia sialis*). Directly relating snag density to cavity-nester reproduction (Lloyd and Slater 2007) and incorporating stand age (Zarnowitz and Manuwal 1985, Saab et al. 2007) can create more specific management guidelines for early successional forests by providing estimates of snag densities needed for high quality habitat combined with how long a stand may be used post disturbance.

Habitat management is often critical for maintaining habitat quality for species that require disturbance-dependent ecosystems (Hunter et al. 2001), but management can sometimes have unintended negative consequences by altering food availability (Shochat et al. 2005), individual behavior (Patten and Kelly 2010), or predation events (Hawlena et al. 2010). Further, human-modified landscapes may be more likely to have occupancy decoupled from habitat quality (Van Horne 1983, Bock and Jones 2004). Because the types of management and disturbance used to maintain habitat for early successional birds can vary considerably, e.g., clearcuts, partial harvesting, and prescribed burning (Perry and Thill 2013, Versluijs et al. 2017), measurements of reproduction, e.g., nest success and productivity, or survival along with occupancy or abundance

(Chalfoun and Martin 2007, Devries et al. 2018), should be used to interpret habitat quality (Garshelis 2000). This may then help identify situations where it is appropriate to use occupancy or abundance to inform management.

The Southeastern American Kestrel (*Falco sparverius paulus*; hereafter, southeastern kestrel) is a secondary cavity nester associated with open habitats, such as longleaf pine (*Pinus palustris*), sandhill, and early successional forest, characterized by short vegetation interspersed with trees, snags, or other artificial structures that could be used for hunting perches or nest sites (Smallwood 1987, Hoffman and Collopy 1988, Miller et al. 2019). However, knowledge of southeastern kestrel occupancy and reproduction in early successional forests and their relationship to stand age, stand size, and snag density is limited. Populations of American Kestrels (*Falco sparverius*; hereafter, kestrel) across North America have been declining for decades (Farmer and Smith 2009, McClure et al. 2017). The southeastern kestrel suffered an estimated 82% decline during the previous century in Florida (Hoffman and Collopy 1988) and is state-listed as threatened (FWC 2013). Data from the Breeding Bird Survey in the Peninsular Florida Bird Conservation Region (Sauer et al. 2020) indicate a negative, non-significant population change from 1980–2019: $\beta = -0.88$, 95% CI (-2.50, 0.64). The southeastern kestrel occurs primarily in Florida, but is also patchily distributed in the coastal plain of neighboring states (FWC 2003, Schneider et al. 2010). One of the largest remaining populations of this subspecies resides in early successional forest in peninsular Florida (FWC 2013). Additionally, our knowledge of this subspecies is largely driven by nest-box studies (Smallwood et al. 2009, Brown et al. 2014, Miller et al. 2019). Although nest boxes are an important management tool (Toland and Elder 1987, Smallwood and Collopy 2009), an understanding of southeastern kestrel occupancy and reproduction in natural cavities of varying snag sizes and densities is needed (McClure et al. 2017).

We had two objectives to assess southeastern kestrel occupancy and reproduction in early successional forest. Our first objective was to determine how stand age, stand size, and snag density explain southeastern kestrel occupancy, nest survival, and productivity (the number of young fledged per successful nest) and we made several predictions. First, we expected southeastern kestrel occupancy to decline as stands age because southeastern kestrels prefer open habitat characterized by short vegetation (Smallwood 1987, Miller et al. 2019) and the early successional forest at our study site exhibits rapid regrowth after disturbance (Myers 1990). Second, we expected southeastern kestrel occupancy to increase with stand size because kestrels may prefer large habitat patches for nesting, presumably to ensure availability of sufficient prey resources (Smallwood et al. 2009). Third, we expected southeastern kestrel occupancy to increase with snag density because kestrels require habitat containing structures that can be used for hunting perches and nest sites (Hoffman and Collopy 1988). Our second objective was to evaluate the relationship between southeastern kestrel occupancy and reproduction (i.e., nest success and survival, and productivity) because habitat management at our study site may not have effectively mimicked natural disturbance regimes needed for cavity nesters (Greenberg et al. 1995), and the decoupling of occupancy and reproduction is most likely to occur in human-modified landscapes (Van Horne 1983). Yet theory often assumes

that individuals should behave adaptively (i.e., use behaviors associated with increased fitness) by selecting high quality habitat and using low quality habitat only when no high quality habitat occurs or when the habitat has become exceedingly crowded (Fretwell and Lucas 1970, Petit and Petit 1996, Martin 1998). We therefore expected that habitat with a higher probability of occupancy would be higher quality habitat, in terms of nest survival and productivity.

METHODS

Study site

We surveyed southeastern kestrels during the 2018–2019 breeding seasons (April to June) in sand pine (*Pinus clausa*) scrub habitat in Ocala National Forest (Ocala NF), Florida (Fig. 1). Ocala NF contains ~89,000 ha of sand pine scrub (USFS 1999) and is the largest remaining expanse of Florida scrub, an ecosystem endemic to Florida (Myers 1990). Florida scrub is a xeromorphic shrub community dominated by scrubby evergreen oaks (*Quercus* spp.) and Florida rosemary (*Ceratiola ericoides*), which eventually succeeds to sand pine forest when fires are suppressed (Myers 1990; Fig. 2). It is a fire-resilient community, meaning individual sand pines burn easily, but the community readily regenerates after a high intensity fire (Myers 1990).

Fig. 1. Southeastern American Kestrel (*Falco sparverius paulus*) nests, all early successional stands (≤ 15 years old), and stands with point-count surveys in Ocala National Forest, Florida, USA, 2018–2019.

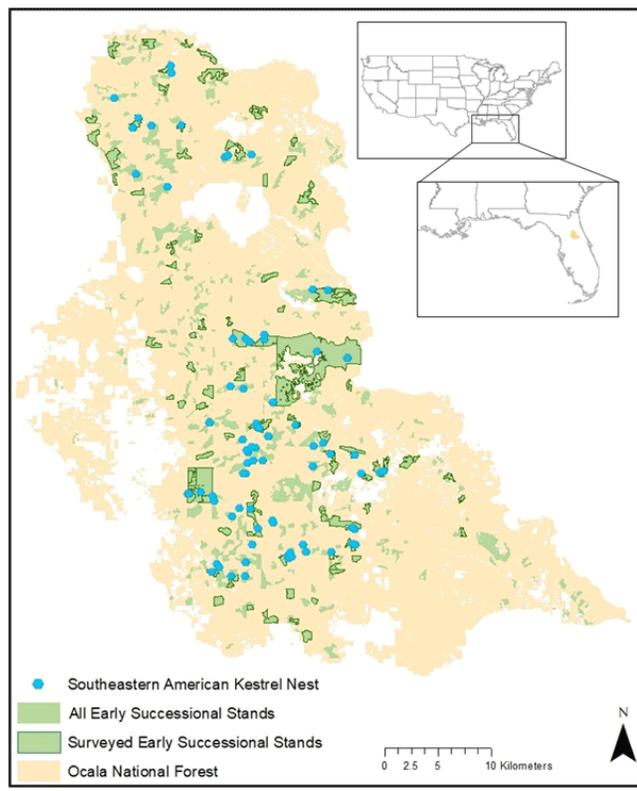


Fig. 2. Early successional sand pine (*Pinus clausa*) scrub stands in Ocala National Forest, Florida, USA, (A) 2 years, (B) 6 years, and (C) 10 years since treatment. (D) A 3-year-old stand with moderate snag density. (E) A Southeastern American Kestrel (*Falco sparverius paulus*) nest cavity in a sand pine snag checked by a researcher with a nest-inspection camera.



Sand pine in Ocala NF is intentionally regenerated for pulpwood and managed as a patchy mosaic for forest products, wildlife habitat, and recreation (USFS 1999). Early successional habitat (defined here as ≤ 15 years old; USFS 1999, Miller and Shea 2021) for southeastern kestrels thus occurs in hundreds of clearcut stands of regenerating scrub embedded within an extensive matrix of older sand pine forest (Fig. 1). These stands are created and maintained by either a clearcut, a clearcut followed by prescribed burn, or wildfire, which may be followed by roller chopping and reseedling (USFS 1999, Hinchee and Garcia 2017). Here, for simplicity, we reference sites as prescribed burns or wildfires if they received these treatments regardless of what other management occurred. One of two wildfire stands was also partially salvage logged. Sand pine stands designated for commercial harvesting are usually cut before they reach 55 years old. Managers aim to leave ≥ 2.5 snags/ha in clearcuts and at least 5–10 snags/ha in salvage logged sites (USFS 1999). Snags may be knocked down during harvesting if in the way of equipment.

Study species

The southeastern kestrel is a non-migratory subspecies of American Kestrel (Hoffman and Collopy 1988). Southeastern kestrels cannot be reliably distinguished in the field from the northern subspecies that overwinters in Florida (*Falco sparverius sparverius*), but the northern subspecies does not breed in Florida (Smallwood and Bird 2002). The kestrel incubation period lasts approximately 30 days and fledging occurs at about 28 days post hatching (Smallwood and Bird 2002).

Occupancy

We used a stratified-randomized sampling scheme to survey early successional stands (≤ 15 years old) across Ocala NF. We first categorized all stands by stand size, treatment (prescribed burn, wildfire, or clearcut without fire, hereafter clearcut), and stand age (years since last treatment of the stand; Fig. 2). We then stratified sampling across early successional stands based on stand age (Table 1) and stand size to randomly select stands to survey within each age and size category. We calculated stand size as hectares of continuous sand pine scrub habitat ≤ 15 years old (excluding dirt roads between stands; range = 19.0–2981.1 ha, median = 124.70 ha). During the first year of surveys we did not detect any southeastern kestrels in early successional stands > 10 years old, and therefore in the second year we conducted point counts (Ralph et al. 1995) only at stands ≤ 10 years old. We did not stratify surveys by treatment because of the few prescribed burn and wildfire stands available for sampling (Table 1).

Table 1. Number of point-count stations in Ocala National Forest, Florida, USA, April to June 2018–2019, stratified by stand age and categorized by treatment. Prescribed burn and wildfire points were limited by the number of stands available.

Time since treatment (years)	Clearcut	Prescribed Burn	Wildfire	Total
1–3	15	11	0	26
4–6	24	9	6	39
7–9	17	0	2	19
10–12	10	1	5	16
13–15	4	0	0	4
Total	70	21	13	104

We conducted 416 paired point counts at 104 point-count stations across 81 stands to determine occupancy of southeastern kestrels during the breeding season (survey dates: 9 April to 15 June 2018 and 15 April to 20 June 2019; Fig. 1). A point-count station consisted of two paired points spaced 250 m apart. Two observers conducted point counts simultaneously, one at each of the paired points within a point-count station. The observers then swapped positions and did a second point count. Each point count was 10 minutes in duration. Occupancy modeling requires repeated sampling at each site to estimate detection probability (the probability of detecting a species that is present) and the accuracy and precision of occupancy estimates increases with the number of sampling occasions (MacKenzie et al. 2002). We used this point-count method to double the number of sampling occasions, ensure that both observers surveyed at every point, and to increase the likelihood of closure, which is a key assumption of occupancy modeling (Rota et al. 2009). We visited each point-count station a second time in the latter half of the breeding season (starting 15 May 2018 and 20 May 2019). We repeated the two paired point-count surveys, resulting in each station being surveyed four times in total. Each point-count station was spaced at least 1 km apart within years to avoid double-counting and ensure independent observations between stations. In the second year, point-count stations were placed in new locations to increase spatial replication and increase representation of environmental gradients (e.g., stand age).

We conducted point counts in the three hours after dawn. During counts, we recorded all southeastern kestrels detected visually or

aurally within 200 m. However, not all stands were large enough to accommodate the 200-m radius. To account for this, we calculated the area of forest sampled for each point count (8.1–12.6 ha, where 12.6 ha is the area sampled in a 200-m radius) to use as a covariate. We estimated distance from point-count center to the kestrel for every detection using a laser rangefinder (Nikon Prostaff 550, 0.5-m precision). The radius of the two point counts within a point-count station overlapped, but we counted a detection if at least one of the two points had a kestrel detection.

Nest survival

To determine nest survival, we used targeted nest searching at > 125 early successional stands each year (Fig. A1.1), including all stands containing point counts ($N = 81$). All accessible prescribed burn stands were searched ($N = 19$). There were only two wildfire stands and both were ≥ 5 years old and very large (> 3000 ha total). Accessible portions of the wildfire stands were searched both years. Nest searching was not timed or restricted to transects. Instead, targeted nest searching involved walking through accessible parts of the stand and stopping frequently to scan with binoculars for as long as necessary to thoroughly search each stand. We searched stands containing point counts for nests regardless of whether kestrels were detected during point-count surveys. This was to ensure that we did not miss kestrels nesting in parts of the stand not included within the radius of the point count. We monitored nests with nest-inspection camera tools (<https://www.ibwo.org>, David Luneau, Arkansas, USA) when possible. The camera was attached to a telescoping pole that could be extended up to 15.2 m (Fig. 2). The camera transmitted wirelessly to a handheld monitor where images and video could be recorded. When nests were occasionally inaccessible with camera tools (e.g., because of windy conditions; $N = 4$), we observed for 20 minutes per visit and used adult southeastern kestrel behavior (Willoughby and Cade 1964) to determine if the nest was still active, and the stage of nesting (Martin and Geupel 1993), if possible. For example, if it had been > 30 days since a full clutch was laid and parents were still inside the cavity or if parents were observed bringing food to the cavity with no adults inside, we assumed the nest had nestlings. We monitored nests at regular seven-to-10-day intervals when possible until the nest fledged or failed. We estimated date of incubation initiation by observing an unfinished clutch or by backdating from the observed or inferred hatching date (Smallwood and Smallwood 1998). A nest was considered successful if at least one nestling reached ≥ 20 days old (Smallwood and Smallwood 1998, Gault et al. 2004, Smallwood 2016). We could not use the nest-inspection camera tool past this date because of the risk of causing premature fledging. Productivity was assessed on the same day a nest was considered successful by counting the number of nestlings.

Habitat measurements

We constructed plots centered on point-count and nest-site locations in 2018 and 2019 to assess habitat characteristics and capture structural variation in habitat from successional dynamics, including maximum shrub height, percent bare ground, sand pine cover, snag density, and snag size. We defined snag density (snags/ha) as the number of snags > 8 cm diameter at breast height (dbh) in one 250×100 m transect (for point counts) or two $100\text{--}250$ m \times 100 m transects (for nests) originating from the point count or nest, divided by the area sampled. Two transects were used for nests to be able to redirect transects that would

otherwise run into the boundary of the stand. We measured snag density by transects as a proxy for measuring the true snag density of the stand. We categorized snags by size (1–3) based on estimated snag dbh and biological relevance for kestrels: 1 (perches; 8–15.9 cm), 2 (possible nesting; 16–24.9 cm), 3 (preferred nesting; ≥ 25 cm; Hoffman 1983). We used size categories rather than measuring the exact dbh for each snag because of the large number of snags observed. Snag density also was calculated for snags ≥ 25 cm dbh (hereafter, large snag density) because southeastern kestrels prefer these snags for nest sites (Hoffman 1983). At each confirmed nest snag, we also measured snag dbh, cavity height, snag height, and whether the cavity was natural or excavated (Martin et al. 1997).

We calculated the amount of early successional habitat (≤ 15 years old) within 1 km and 5 km of the nest or point count using USFS maps and harvesting data (USFS 2019) because southeastern kestrel occupancy and reproduction can be related to the amount of nearby habitat in the landscape (Touihri et al. 2019). We chose these buffer sizes because 1 km reflects the approximate size of southeastern kestrel home ranges (Smallwood and Bird 2002) and 5 km approximates the median natal dispersal distance for southeastern kestrels in Florida (4.9 km; Miller and Smallwood 1997). We did all calculations of habitat amount and stand size in ArcMap 10.8 (ESRI 2020).

Analysis

We used single-season occupancy models to estimate southeastern kestrel occupancy probability based on environmental covariates (MacKenzie et al. 2002). Occupancy models allow for the estimation of species occurrence when detection is imperfect and require repeated sampling to estimate detection. Species occurrence and detection probability were modeled as a function of a four-occasion encounter history based on the four point-count station surveys. Each paired point-count survey resulted in the binary response of Y_{ij} , southeastern kestrel detection ($Y = 1$) or non-detection ($Y = 0$) at site i during visit j . For example, an encounter history of 1010 at site i would indicate that a southeastern kestrel was detected during the first and third surveys but not in the second or fourth surveys.

We considered the following covariates in occupancy models: stand age, three measures of habitat (stand size and the amount of early successional habitat, ≤ 15 years old, within 1 km and 5 km of the point count), distance to nearest road (including dirt roads), distance to stand edge, snag density, large snag density, survey year, and treatment (whether the stand was classified as a clearcut, prescribed burn, or wildfire). Survey year was tested to account for unexplained annual variation in the environment. Detection covariates measured included time of day and Julian date to account for potential variation in detection probability (Mackenzie et al. 2002). Birds may vocalize more or have increased activity at different times of the morning or across the breeding season, resulting in changes in detection probability between surveys (Furnas and Callas 2015). To account for stands that were smaller than the 200-m point-count radius we included the natural log of the area of each point count (8.1–12.6 ha) in all models. We included stand age as a quadratic term to allow for nonlinear relationships between stand age and occupancy probability. We expected possible nonlinear relationships because other early successional species in this system exhibit non-linear patterns of

occupancy or abundance (Beatty 2019, Miller and Shea 2021) and because southeastern kestrel occupancy may be dependent on responses of excavator species (Blanc and Walters 2008).

We used generalized linear models (GLMs) to assess the effects of habitat type and specific habitat characteristics on nest daily survival rate (DSR) and productivity. GLMs for DSR used a logistic-exposure modeling framework with a binomial distribution that accounts for variation in exposure of each nest (Shaffer 2004). Productivity models were fit with a GLM using a log link function and assuming a Poisson error distribution. We estimated nest success by calculating DSR and raising survival rate to the power of the observed length of the nest cycle (30 days incubation + 20 days to success was determined: DSR^{50}). Covariates included were the same as described for occupancy, with the addition of incubation initiation date, cavity height, snag dbh, and the exclusion of nonlinear effects of stand age. Kestrels may have a delay in finding and occupying new nest sites (Brown et al. 2014), but given kestrels' preference for short vegetation (Smallwood 1987, Miller et al. 2019) and the rapid regrowth of vegetation at Ocala NF (K. Miller, *personal observation*) we might expect linear relationships with increasing stand age. We included incubation initiation date into all DSR and productivity models to account for potentially reduced nest success of nests started later in the season (Smallwood and Bird 2002, Steenhof and Heath 2013, but see Touihri et al. 2019).

To increase parsimony for all modeling, we first tested all covariates in univariate models and only included significant covariates, i.e., where the 95% confidence interval (CI) for the parameter estimate did not overlap zero, in final model selection. To fulfill our objectives, we included a linear or quadratic term for stand age, both measures of snag density, and the best performing covariate of habitat amount from univariate model selection regardless of significance. We tested for additive effects between all remaining covariates and interactive effects between stand age and habitat amount, and stand age and snag density. We included interactive effects because covariates are not mutually exclusive; the effect of stand age may be dependent on habitat amount or snag density. We tested for correlation among covariates and did not use covariates with $r > |0.4|$ in the same model. We did not consider different measures of snag density (> 8 cm and > 25 cm dbh) in the same model to reduce multicollinearity in model fitting. We centered and scaled continuous covariates (R Core Team 2021) and ranked models using Akaike's information criteria corrected for small sample sizes (AIC_C ; Burnham and Anderson 2004). Models $< 2 AIC_C$ units from the top model were considered competitors.

Correlations between estimates of occupancy probability and nest survival from the top ranked models were tested using Spearman's rank correlation coefficient. To account for variation in uncertainty in estimates, we used a parametric bootstrap (assuming a beta distribution). Nests and point counts were paired together for correlation if they were located in the same continuous stand of the same age (i.e., a nest and point count located in the same three-year-old stand would be paired).

All analyses were run in R version 4.0.3 (R Core Team 2021). R packages used for analyses include unmarked for occupancy models (Fiske and Chandler 2011) and MuMIn for model selection (Bartoń 2002).

Table 2. Comparison of single-season occupancy models to determine the relationship between Southeastern American Kestrel (*Falco sparverius paulus*) occupancy and environmental covariates based on point counts conducted in Ocala National Forest, Florida, USA, April to June 2018–2019. We compared models using log-likelihood (LL), Akaike’s Information Criterion corrected for small sample sizes (AICc), and AICc weights. We also report the number of parameters (*K*) and model differences (Δ AICc). The 10 models with the lowest AICc value out of 19 tested models and the null model are shown. All models also contain the natural log of the amount of habitat surveyed during the point count within 200 m as an occupancy covariate and survey date as a detection covariate. Snag density refers to snags > 8 cm dbh. Large (Lg) snag density refers to snags \geq 25 cm dbh. Habitat5km is the amount of early successional sand pine (*Pinus clausa*) scrub \leq 15 years old within 5 km of the point count.

	Model	<i>K</i>	LL	AICc	Δ AICc	Weight
1	Stand Age ² × Snag Density	8	-123.20	263.9	0.00	0.395
2	Stand Age ² × Lg Snag Density	8	-123.89	265.3	1.39	0.197
3	Stand Age ² × Snag Density + Habitat5km	9	-123.05	266.0	2.09	0.138
4	Stand Age ² × Lg Snag Density + Habitat5km	9	-123.69	267.3	3.37	0.073
5	Stand Age ² + Lg Snag Density	7	-126.07	267.3	3.39	0.073
6	Stand Age ² × Habitat5km + Lg Snag Density	9	-123.90	267.7	3.81	0.059
7	Stand Age ² + Habitat5km + Lg Snag Density	8	-125.96	269.4	5.53	0.025
8	Stand Age ² + Snag Density	7	-127.57	270.3	6.39	0.016
9	Stand Age ² × Habitat5km + Snag Density	9	-125.27	270.4	6.53	0.015
10	Lg Snag Density	5	-130.38	271.4	7.46	0.009
11	Null	2	-139.90	283.9	20.01	0.000

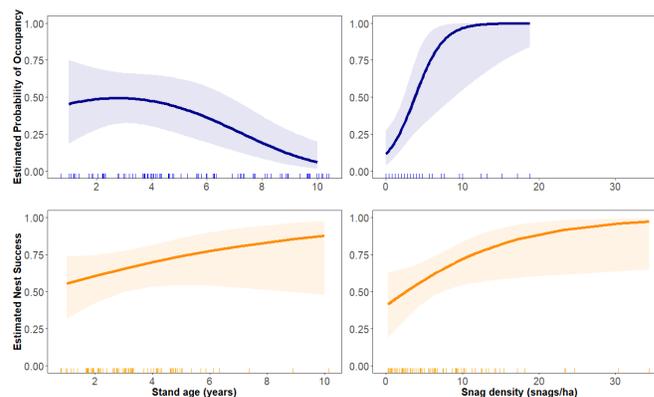
RESULTS

Occupancy

Kestrels were detected at 29 of 104 (28%) point-count stations and 65 of 80 (81%) kestrel observations were visual detections. Kestrels were detected in stands between one and 10 years old, stands 21.9 to 2981.1 ha in size, with zero to 17.2 snags/ha. Stand age was correlated with % bare ground ($r = -0.51$), pine cover ($r = 0.69$), and shrub height ($r = 0.78$), calculated based on measurements taken at survey locations (Beatty 2019). All measures of habitat amount (stand size and habitat within 1 km and 5 km) were nonsignificant (the 95% CI for the parameter estimates overlapped zero) in univariate model selection, but habitat within 5 km performed best and therefore was used in final model selection. Occupancy had nonsignificant relationships with treatment, survey year, distance to nearest road, and distance to stand edge. These covariates were therefore excluded after univariate model selection.

The top-ranked single-season occupancy model included the following: stand age ($\beta_{\text{standage}} = -1.10$, 95% CI [-1.81, -0.39]), stand age² ($\beta_{\text{standage}^2} = -0.57$, 95% CI [-1.27, 0.12]), snag density ($\beta_{\text{snagdensity}} = 2.26$, 95% CI [0.67, 3.85]), and their interaction ($\beta_{\text{standage}^2 \times \text{snagdensity}} = -1.40$, 95% CI [-2.57, -0.23]) as occupancy covariates. This model included date ($\beta_{\text{date}} = 0.44$, 95% CI [0.05, 0.83]) as a detection covariate (Table 2, Table A1.1). The amount of early successional habitat (\leq 15 years old) within 5 km of the point count was a relatively poor predictor of occupancy ($\beta_{\text{habitat5km}} = 0.18$, 95% CI [-0.46, 0.81]). Occupancy had a nonlinear relationship with stand age and was positively correlated with snag density (Fig. 3). Occupancy probability was overall higher and peaked in older stands as snag density increased but declined with stand age when snag densities were low (Fig. 4). The second-ranked model contained the same covariates, except it included only snags > 25 cm dbh ($\beta_{\text{lg snagdensity}} = 2.26$, 95% CI [0.63, 3.88]). It showed similar support based on AIC_c, although the log-likelihood was lower.

Fig. 3. Partial predictions of estimated occupancy probability and nest success for Southeastern American Kestrels (*Falco sparverius paulus*) in Ocala National Forest, Florida, USA, during 2018–2019 according to the best performing models, based on varying stand age (left) and snag density (right). All other covariates were held at their mean values. Nest success is estimated by raising daily survival rate to the power of the length of the nest cycle observed (approximately 50 days). Shaded areas represent 95% prediction intervals. The relationship between stand age and nest survival was weak ($\beta_{\text{standage}} = 0.32$, 95% CI [-0.09, 0.79]). Maximum snag density at point counts was 18.8 snags/ha, but ~6% of nests were found with greater snag densities. Measured stand ages and snag densities sampled for point counts and nests are indicated on the x-axes.



Nest survival and productivity

We located and monitored 85 nests (Table 3). Of these, 81 (95%) were in snags previously excavated by other cavity-nesting species, three (4%) were open entrances at the top of the snag created by the snag breaking at the crown and becoming hollowed out from

decay, and one (1%) was open from the side and top, likely from a combination of a limb falling and the top of the snag breaking. Of 85 nests, 81 (95%) were in ≤ 6 -year-old stands. The oldest stand containing nests (10 years old) was created by a wildfire. Five nests (6%) had higher snag density than the maximum snag density found during point counts (18.8 snags/ha; Fig. 3).

Fig. 4. Estimated probability of a point-count station being occupied by a Southeastern American Kestrel (*Falco sparverius paulus*) according to the best performing model based on stand age at varying observed levels of snag density. Point counts with ≤ 7.5 snag/ha accounted for 90% of all stands surveyed. Estimated with a 95% confidence interval. No kestrels or snags were detected in stands > 10 years old. Point counts were conducted in Ocala National Forest, Florida, USA, during the 2018–2019 breeding seasons.

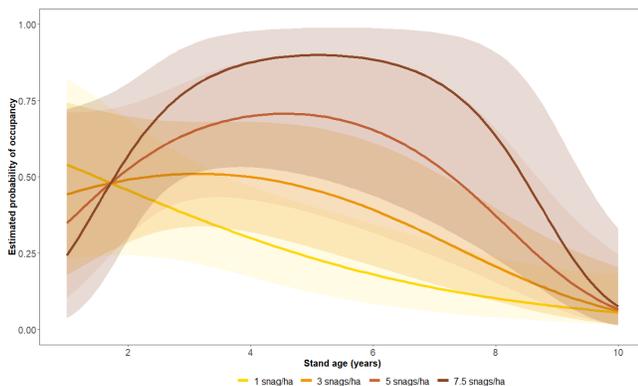


Table 3. Mean, standard deviation, and range of values of nest covariates measured at 85 nests located in Ocala National Forest, Florida, USA, monitored from March to August, 2018–2019. Snag density refers to snags ≥ 8 cm dbh. Large (Lg) snag density refers to snags ≥ 25 cm dbh.

Feature	Unit	Mean	SD	Min	Max
Shrub Height	cm	169.26	73.80	33.7	334.8
Stand Age	years	3.4	1.8	1	10
Stand Size	ha	610.29	907.82	21.9	2981.1
Snag Density	snags/ha	7.20	6.78	0.3	34.4
Lg Snag Density	snags/ha	2.29	2.61	0.0	13.9
Snag Height	m	8.8	2.6	2	17
Cavity Height	m	7.24	2.42	2.1	13.6
Snag dbh	cm	27.52	5.27	17.2	50.8
Incubation Initiation Date	date	16 Apr	20.1	13 Mar	12 Jun

Of the 85 nests, 59 (69%) produced at least one nestling ≥ 20 days old. Apparent nest success was nearly identical in 2018 (69%) and 2019 (70%). Nineteen of 26 failed nests (73%) were assumed depredated because of observations of empty cavities or egg fragments before earliest possible fledge date. Five (19%) were assumed to be depredated and/or abandoned because of eggs covered in dirt or ants or reduced number of eggs, one (4%) failed because of a snag falling over, and one (4%) was colonized by bees (it is unknown if the nest failed before or because of the

bees). Of the three nests with open entrances at the top of the snag, only one failed. The one nest that was open on the top and side was successful.

Nest survival and productivity had nonsignificant relationships with cavity height, snag dbh, survey year, distance to nearest road, distance to stand edge, and treatment. These covariates were therefore excluded after univariate model selection. All measures of habitat amount were nonsignificant in univariate model selection for nest survival, but habitat within 5 km performed best and therefore was used in final model selection. All measures of habitat amount were nonsignificant in univariate model selection for productivity. Stand age was moderately correlated with both stand size and habitat within 1 km ($r > 0.5$) for the productivity dataset and therefore habitat within 5 km was used in final model selection.

The top-ranked model that described DSR contained stand age ($\beta_{\text{standage}} = 0.32$, 95% CI [-0.09, 0.79]), snag density ($\beta_{\text{snagdensity}} = 0.71$, 95% CI [0.12, 1.46]), and incubation initiation date ($\beta_{\text{nestinc}} = -0.48$, 95% CI [-0.81, -0.14]; Table 4, Table A1.2). The next three models were < 2 AIC_C units from the top model. The second highest ranked model contained snag density without stand age. The third and fourth ranked models contained snag density, stand age, and the amount of early successional habitat within 5 km of the nest ($\beta_{\text{habitat5km}} = 0.26$, 95% CI [-0.14, 0.66]). DSR was positively correlated with snag density (Fig. 3). DSR had weak positive relationships with stand age and habitat amount.

Productivity ranged from one to four nestlings and averaged 2.6 ± 1.05 SD ($N = 55$ successful nests). Only one model describing productivity performed better than the intercept model and it included only one covariate, incubation initiation date ($\beta_{\text{nestinc}} = -0.16$, 95% CI [-0.33, 0.01]; Table 5, Table A1.3).

Occupancy versus nest survival

Occupancy probability and nest survival had a low, but significant, positive correlation across stands ($r = 0.27$, CI [0.03-0.50], $N = 27$). The correlation was strongest in clearcuts ($r = 0.38$, CI [0.02-0.71], $N = 14$). There was no correlation in prescribed burns ($r = 0.29$, CI [-0.2 - 0.73], $N = 9$) or wildfires ($r = -0.01$, CI [-0.8 - 0.8], $N = 4$). Estimated nest survival tended to be higher in wildfires for a given occupancy rate than for prescribed burns or clearcuts (Fig. 5).

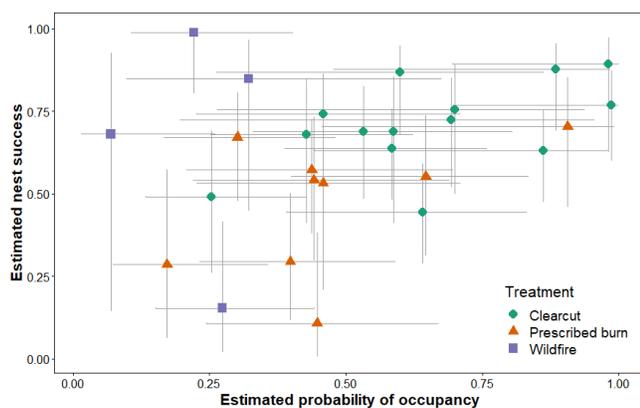
DISCUSSION

Understanding the role of stand age, stand size, and snag density is important for the conservation of cavity-nesting birds in early successional forests. We found different effects of these factors on occupancy and reproduction. Occupancy probability quickly declined in older early successional stands, such that stands > 7 years old were rarely used by kestrels and no kestrels were detected in stands > 10 years old. Importantly, an increase of just a few snags/ha corresponded with a large increase in occupancy for a given stand age. However, stand age was not a good predictor of nest survival and could be a misleading indicator of habitat quality without also considering snag density. We discuss the effects on occupancy, reproduction, and their interactions in the context of conservation and management.

Table 4. Comparison of generalized linear models to determine the relationship between Southeastern American Kestrel (*Falco sparverius paulus*) nest daily survival rate and environmental covariates. The top model best predicts the probability that a nest will survive each day. We compared models using log-likelihood (LL), Akaike’s Information Criterion corrected for small sample sizes (AICc), and AICc weights. We also report the number of parameters (*K*) and model differences (Δ AICc). The 10 models with the lowest AICc value out of 20 tested models and the null model are shown. Date is the incubation initiation date. Snag density refers to snags ≥ 8 cm dbh. Habitat5km is the amount of early successional sand pine (*Pinus clausa*) scrub ≤ 15 years old within 5 km of the nest. Nests were located in Ocala National Forest, Florida, USA, and monitored from March to August, 2018–2019.

Model	<i>K</i>	LL	AICc	Δ AICc	Weight
1 Stand Age + Snag Density + Date	4	-74.98	158.1	0.00	0.194
2 Snag Density + Date	3	-76.11	158.3	0.20	0.176
3 Stand Age + Habitat5km + Snag Density + Date	5	-74.13	158.5	0.39	0.160
4 Habitat5km + Snag Density + Date	4	-75.48	159.1	1.00	0.118
5 Stand Age x Snag Density + Date	5	-74.96	160.1	2.04	0.070
6 Habitat5km + Date	3	-77.13	160.4	2.25	0.063
7 Stand Age x Habitat5km + Snag Density + Date	6	-74.09	160.5	2.41	0.058
8 Stand Age x Snag Density + Habitat5km + Date	6	-74.11	160.5	2.43	0.058
9 Date	2	-78.30	160.6	2.54	0.055
10 Stand Age + Habitat5km + Date	4	-76.38	160.9	2.82	0.048
11 Null	1	-83.28	168.6	10.47	0.001

Fig. 5. The correlation between probability of occupancy and estimated nest success at 27 Southeastern American Kestrel (*Falco sparverius paulus*) nests and point counts in Ocala National Forest, Florida, USA, 2018–2019, grouped by stand treatment. Nest success is estimated by raising daily survival rate to the power of the length of the nest cycle observed (approximately 50 days). Grey lines represent the 95% confidence interval. Point counts and nests located in the same continuous stand of the same age were used. There was a low positive correlation among all stands ($r = 0.27$, CI [0.03–0.50], $N = 27$). The correlation was strongest when in clearcuts ($r = 0.38$, CI [0.02–0.71], $N = 14$). There was no correlation in prescribed burns ($r = 0.29$, CI [-0.2–0.73], $N = 9$) or wildfires ($r = -0.01$, CI [-0.8–0.8], $N = 4$).



Occupancy

The duration of early successional forest varies across different forests and management strategies (Swanson et al. 2011), and therefore relationships between cavity nesters and stand age may also be expected to vary across regions. Kestrels and many early

successional cavity nesters in the Northwestern U.S. and western Canada prefer stands one to four years post fire (Hobson and Schieck 1999, Saab et al. 2004, but see Saab et al. 2007). As stands increase in age they become lower quality habitat for kestrels because there is less open ground and taller vegetation (Smallwood 1987, Smallwood and Collopy 2009, Miller et al. 2019). At snag densities of ≤ 7.5 snags/ha, southeastern kestrel occupancy tended to peak in stands ≤ 5 years old (Fig. 4). Habitat suitability may be brief because of the relatively low snag density in sand pine scrub (Outcalt and Greenberg 1998) and the clearcutting and seeding techniques used in Ocala NF that can speed up successional dynamics (Swanson et al. 2011, Hinchee and Garcia 2017).

Stand age is an important metric for many bird species in early successional habitat (Schlossberg and King 2009, Matseur et al. 2019, Versluijs et al. 2020, Miller and Shea 2021), but for cavity-nesting birds, stand age is more informative when used in conjunction with snag density (Zarnowitz and Manuwal 1985, Barry et al. 2018, Martin et al. 2021). For example, our occupancy model predicted that if there were 5 snags/ha, there was a 70% probability of occurrence (per point) in a four-year-old stand. However, given only 1 snag/ha, expected occupancy probability dropped to just 30%. Allowing for nonlinear relationships with stand age also identified a potential lag between disturbance and stand colonization. This could be because of kestrels’ reliance on excavators to first create cavities (Blanc and Walters 2008) or a delay in kestrels finding and using new nesting sites (Brown et al. 2014).

Nest survival and productivity

Stand age may not be a reliable indicator of habitat quality for cavity nesters (Holt and Martin 1997, Saab et al. 2007, Stillman et al. 2019, Martin et al. 2021). Stand age, although a strong predictor of occupancy, was a relatively weak predictor of nest survival for southeastern kestrels. Vegetative characteristics may influence kestrel reproduction (Smallwood and Wargo 1997, but see Miller et al. 2019), but the presence of snags or nesting cavities may mitigate reduced habitat quality in older stands (Sheffield et

Table 5. Comparison of generalized linear models to determine the relationship between Southeastern American Kestrel (*Falco sparverius paulus*) nest productivity and environmental covariates. We compared models using log-likelihood (LL), Akaike's Information Criterion corrected for small sample sizes (AICc), and AICc weights. We also report the number of parameters (*K*) and model differences (Δ AICc). The 10 models with the lowest AICc value out of 20 tested models are shown. Date is the incubation initiation date. Snag density refers to snags \geq 8 cm dbh. Large (Lg) snag density refers to snags \geq 25 cm dbh. Habitat5km is the amount of early successional sand pine (*Pinus clausa*) scrub \leq 15 years old within 5 km of the nest. Nests were located in Ocala National Forest, Florida, USA, and monitored from March to August, 2018–2019.

Model	<i>K</i>	LL	AICc	Δ AICc	Weight
1 Date	2	-86.99	178.2	0.00	0.285
2 Null	1	-88.65	179.4	1.17	0.159
3 Habitat5km + Date	3	-86.77	180.0	1.80	0.116
4 Snag Density + Date	3	-86.91	180.3	2.08	0.101
5 Lg Snag Density + Date	3	-86.91	180.3	2.09	0.101
6 Stand Age + Date	3	-86.98	180.4	2.23	0.094
7 Habitat5km + Lg Snag Density + Date	4	-86.70	182.2	3.99	0.039
8 Habitat5km + Snag Density + Date	4	-86.72	182.2	4.03	0.038
9 Stand Age + Habitat5km + Date	4	-86.77	182.3	4.13	0.036
10 Stand Age + Snag Density + Date	4	-86.90	182.6	4.39	0.032

al. 2001). For example, median snag density at point-count locations in stands > six years old was only 0.4 snags/ha, whereas median snag density at nest locations in stands > six years old was 4.76 snags/ha, indicating that southeastern kestrels are selecting the rare patches of high snag density in older stands for nesting. Stand age is frequently used to assess changes in abundance, occupancy, and reproduction of cavity nesters post disturbance (Smucker et al. 2005, Hutto and Gallo 2006, Saab et al. 2011), but we found interpreting stand age without considering the role of snag density may lead to under- or overestimating habitat quality of older stands.

Increasing snag density may relate to an increase in DSR for cavity-nesting birds because of a decrease in predation probability. In this study, most nest failures (at least 73%) were assumed to be caused by predation. Predation cannot be separated from abandonment without continuous observation of the nest, but rates of abandonment are typically low for kestrels and unaffected by researcher disturbance (Smallwood 2016). We therefore assume that failures were likely because of predation. As snag density decreases, secondary cavity nesters may be left with older and fewer cavities of potentially lower quality. Secondary cavity nesters generally have lower nest success than primary cavity nesters and may be more likely to be nest-site limited (Li and Martin 1991, Johnson and Kermott 1994, Brightsmith 2005, Miller 2010). Increasing numbers of snags and cavities may force cavity-nest predators to search more cavities to find a nest (Martin 1988, Martin and Roper 1988). Lower nest success may be a result of increased predation at older cavities because a predator may have previously depredated the cavity and learned its location (Sonerud 1989, Miller 2002).

Larger snags provide important foraging (Nappi et al. 2003, Dufour-Pelletier et al. 2020) and nesting (Conner et al. 1975, Saab et al. 2009, Cross et al. 2021) opportunities and the value of retaining large snags to improve habitat quality for cavity-nesting birds has long been identified (Zarnowitz and Manuwal 1985, McComb et al. 1986). We found that 67% of southeastern kestrel nesting snags were > 25 cm dbh. However, measures of snag density for kestrels should also include small snags (< 16 cm dbh)

not suitable for nesting because small snags can also be important for occupancy or reproduction, e.g., hunting perches (Sheffield et al. 2001).

Stand size may be less important for habitat quality when foraging sites are located outside of breeding habitat patches (Estades 2001) or after a certain size threshold has been reached (Schlossberg and King 2007). Cavity nesters are generally less sensitive to the effects of reduced stand size caused by fragmentation than ground or tree nesters (Lampila et al. 2005), likely because of reduced predation pressure in cavities, but this may not extend to secondary cavity nesters (Martin 1995). Efforts to assess the relationship between kestrel reproduction and territory- and landscape-scale habitat variables have found mixed results (Miller et al. 2019, Touihri et al. 2019). Kestrels in rural landscapes occupied nest boxes at higher rates in large contiguous patches (> 1000 ha) than smaller patches (Smallwood et al. 2009), but the relationship between stand size and occupancy may vary with patch quality. Lesser Kestrels (*Falco naumanni*) can extend their foraging distance when surrounded by habitat of lower quality, resulting in reductions in foraging rates, nestling fitness, and fledging success (Catry et al. 2013). Southeastern kestrels nesting in late successional stands in Ocala NF sometimes foraged in adjacent stands that were relatively younger (M. Beatty, *personal observation*), but for occupancy of early successional stands in our study the interaction between stand age and stand size was not significant.

Treatment (i.e., whether the stand was classified as a clearcut, prescribed burn, or wildfire) did not have a significant relationship with either occupancy probability or nest survival. This was surprising, but the lack of effect may be driven, in part, by our small sample size of wildfires and prescribed burns, which was because of their relative rarity in the study area. Greenberg et al. (1995) determined that clearcuts can potentially mimic the vegetative structure created by burns in scrub environments, but acknowledged that this may not include differences in snag retention and creation. Unlogged and partially salvage-logged burns are important nesting and foraging habitat for cavity nesters (Kotliar et al. 2002, Hutto and Gallo 2006, Hutto et al. 2020).

Given that the oldest stand where nesting occurred was created by wildfire and that prescribed burns will be used more frequently in Ocala NF (Hinchee and Garcia 2017), it would be helpful to assess southeastern kestrel nest success and occupancy in burned stands of varying ages and snag densities as they become available.

Southeastern kestrel productivity (the number of young fledged per successful nest) did not have a strong relationship with any measured covariate. Changes in food availability post fire (Dawson and Bortolotti 2006) and rainy weather during the nestling stage (Smallwood and Natale 1998) have been suggested to affect productivity. We note that we assessed nest success and productivity before the expected fledge date (> 20 days versus 28 days), which is common for kestrel studies (Smallwood and Smallwood 1998, Gault et al. 2004, Steenhof and Newton 2007, Smallwood 2016). Although truncating this assessment date may lead to an overall bias of higher survival estimates, we have no reason to expect bias across the environmental gradients we considered.

Finally, it is important to consider that all of our nests were in natural cavities, yet kestrels also frequently use nest boxes. Our estimates for nest success were similar to nest success reported from nest-box studies in peninsular Florida by Smallwood and Collopy (2009; 67.4%) and Miller et al. (2019; 65%).

Occupancy versus nest survival

When abundance or occupancy are correlated with successful reproduction, estimating abundance or occupancy can be a useful substitute for estimating reproduction (Bock and Jones 2004). We expected that habitat with a higher probability of occupancy was higher quality habitat (Fretwell and Lucas 1970). We found that occupancy probability and estimated nest success and survival had a low positive correlation in clearcut stands (Fig. 5). This positive correlation provides an example of where occupancy could be a useful substitute for measuring reproduction in clearcuts in this system (Bock and Jones 2004). We did not find this relationship to be consistent with wildfire stands.

Nests in wildfire stands generally had higher estimated nest success for a given occupancy rate than nests in clearcuts or prescribed burns. This may be a result of management actions that follow treatment. Clearcut stands at Ocala NF are usually reseeded with sand pine after harvesting (USFS 1999), which can increase sand pine density and reduce the longevity of early successional habitat (Swanson et al. 2011). The average sand pine cover at nine- to 10-year-old clearcut point-count stations ($38.9\% \pm 20.9$ SD, $N = 12$) was higher than pine cover at nests in an unseeded wildfire stand of the same age ($5.3\% \text{ cover} \pm 7.7$ SD, $N = 3$). There were no young wildfire stands (< 5 years old) available for us to study and we are therefore limited to comparing relationships in older stands. Open habitat with short vegetation is important for kestrel foraging (Bohall-Wood and Collopy 1986, Smallwood 1987) and the differences in sand pine cover between treatments of the same age may be part of the reason for differences between clearcut and wildfire correlation estimates. Prescribed burn stands may or may not be reseeded, depending on the management goal (Hinchee and Garcia 2017), which may have resulted in inconsistent relationships. Although we did not find a strong relationship between treatment and occupancy or nest survival, the results from the correlation test emphasize

caution when extrapolating predictions across management treatments and suggest that clearcutting in this forest may not completely mimic natural disturbance regimes.

More broadly, these results highlight the value of assessing the relative ability of different predictor variables to reflect both occupancy and fitness relationships. Using stand age alone, we would have concluded that occupancy probability was not a reliable indicator of nest survival and that southeastern kestrels were undervaluing older stands (Gilroy and Sutherland 2007). A qualitatively different conclusion arises when comparing occupancy probability and nest survival based on snag density (Fig. 3). Evaluating habitat quality based on stand age without snag density would be an example of occupancy being a reliable indicator of habitat quality, but the wrong, or an incomplete set of, habitat components being measured. Finding inconsistencies between occupancy and fitness based on the best predictor variables may mean that occupancy is not a reliable indicator of fitness within that system, but it also could mean that another more important variable was not considered or effectively measured. Similar issues arise with what components of fitness are considered when interpreting relationships of fitness and abundance (e.g., Cattau et al. 2016).

In the most extreme scenario, this could lead to the misidentification of an undervalued resource, i.e., high quality habitat that an animal avoids (Gilroy and Sutherland 2007), or ecological trap (Battin 2004). Notably, most ecological-trap studies use observational methods (Hale and Swearer 2016) and therefore rely on the ability of the observer to accurately identify the best predictor variables for habitat selection. It is important to understand how environmental cues influence habitat selection (Patten and Kelly 2010) and to explore the mechanisms relating habitat selection and fitness (Hale and Swearer 2016). Our results emphasize the importance of determining which environmental predictors to use when comparing habitat selection and habitat quality to avoid misinterpreting relationships.

Management implications

Early successional forest provides habitat for a diversity of cavity nesters, but the suppression of natural disturbance events makes them challenging to maintain (Hutto 1995). Recommendations regarding stand age, stand size, and snag density are frequently provided to maintain high quality habitat, but these recommendations may not always be transferrable between different forests (Gibbs et al. 1993) or be consistent between estimates of occupancy and reproduction (Holt and Martin 1997, Saab et al. 2007, Stillman et al. 2019). Southeastern American Kestrels in our study area had overall high nesting success but may have only a short window of opportunity to use sand pine scrub habitat post disturbance (≤ 10 years). Even a slight increase in snag density (an additional 1–2 snags/ha) could help moderate the negative effects of increasing stand age. Managers might explore whether more snags could be retained during clearcutting or whether additional snags might be created through girdling live trees. In addition, it should be noted that ongoing forest-wide scrub restoration at Ocala NF through clearcutting and prescribed burning (Hinchee and Garcia 2017) might result in temporary increases in snag availability but potentially reduce snag availability over the long term. Wildfire stands appear to provide higher quality habitat than clearcuts or prescribed burns,

but our inference was limited because there were few wildfire stands and none was < 5 years old. For Southeastern American Kestrels in this region, we recommend maintaining stands ≤ 10 years old, with an average of ≥ 5 snags/ha and at least one snag/ha > 25 cm in diameter. Our results build on evidence that snag density is an important indicator of habitat quality for cavity-nesting birds and should be considered in combination with stand age to determine how long stands can be occupied post disturbance.

Responses to this article can be read online at:
<https://www.ace-eco.org/issues/responses.php/2261>

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Appendix 1

Supplementary tables and figure from “Snag density and stand age, but not stand size, explain occupancy and reproduction of an imperiled cavity nester in early successional forest” in *Avian Conservation & Ecology*.

Table A1.1. Comparison of all single-season occupancy models used to determine the relationship between Southeastern American Kestrel occupancy and environmental covariates based on point counts conducted in Ocala National Forest, Florida, USA, April to June 2018-2019. We compared models using log-likelihood (LL), Akaike’s Information Criterion corrected for small sample sizes (AICc), and AICc weights. We also report the number of parameters (K) and model differences (Δ AICc). All models also contain the natural log of the amount of habitat surveyed during the point count within 200 m as an occupancy covariate and survey date as a detection covariate. Large (Lg) snag density is snags ≥ 25 cm dbh. Habitat is the amount of early successional sand pine scrub ≤ 15 years old within 5 km of the point count.

	Model	K	LL	AICc	Δ AICc	Weight
1	Stand Age ² × Snag Density	8	-123.20	263.9	0.00	0.386
2	Stand Age ² × Lg Snag Density	8	-123.89	265.3	1.39	0.193
3	Stand Age ² × Snag Density + Habitat5km	9	-123.05	266.0	2.09	0.135
4	Stand Age ² × Lg Snag Density + Habitat5km	9	-123.69	267.3	3.37	0.071
5	Stand Age ² + Lg Snag Density	7	-126.07	267.3	3.39	0.071
6	Stand Age ² × Habitat5km + Lg Snag Density	9	-123.90	267.7	3.81	0.058
7	Stand Age ² + Habitat5km + Lg Snag Density	8	-125.96	269.4	5.53	0.024
8	Stand Age ² + Snag Density	7	-127.57	270.3	6.39	0.016
9	Stand Age ² × Habitat5km + Snag Density	9	-125.27	270.4	6.53	0.015
10	Lg Snag Density	5	-130.38	271.4	7.46	0.009
11	Stand Age ² × Habitat5km	8	-127.14	271.8	7.88	0.007
12	Stand Age ² + Habitat5km + Snag Density	8	-127.46	272.4	8.51	0.005
13	Habitat5km + Lg Snag Density	6	-130.37	273.6	9.70	0.003
14	Stand Age ² + Habitat5km	7	-129.55	274.3	10.34	0.002
15	Stand Age ²	6	-130.76	274.4	10.47	0.002
16	Snag Density	5	-132.03	274.7	10.76	0.002
17	Habitat5km + Snag Density	6	-132.02	276.9	12.99	0.001
18	Null	2	-139.90	283.9	20.01	0.000
19	Habitat5km	5	-137.23	285.1	21.16	0.000

Table A1.2. Comparison of all generalized linear models used to determine the relationship between Southeastern American Kestrel nest daily survival rate and environmental covariates. The top model best predicts the probability that a nest will survive each day. We compared models using log-likelihood (LL), Akaike’s Information Criterion corrected for small sample sizes (AICc), and AICc weights. We also report the number of parameters (K) and model differences (Δ AICc). Date is the incubation initiation date. Habitat is the amount of early successional sand pine scrub ≤ 15 years old within 5 km of the nest. Nests were located in Ocala National Forest, Florida, USA, and monitored from March to August, 2018–2019.

	Model	K	LL	AICc	Δ AICc	Weight
1	Stand Age + Snag Density + Date	4	-74.98	158.1	0.00	0.169
2	Snag Density + Date	3	-76.11	158.3	0.20	0.152
3	Stand Age + Snag Density + Habitat5km + Date	5	-74.13	158.5	0.39	0.139
4	Habitat5km + Snag Density + Date	4	-75.48	159.1	1.00	0.102
5	Stand Age x Snag Density + Date	5	-74.96	160.1	2.04	0.061
6	Habitat5km + Date	3	-77.13	160.4	2.25	0.055
7	Stand Age x Habitat5km + Snag Density + Date	6	-74.09	160.5	2.41	0.051
8	Stand Age x Snag Density + Habitat5km + Date	6	-74.11	160.5	2.43	0.050
9	Date	2	-78.30	160.6	2.54	0.047
10	Stand Age + Habitat5km + Date	4	-76.38	160.9	2.82	0.041
11	Stand Age + Date	3	-77.88	161.9	3.75	0.026
12	Lg Snag Density + Habitat5km + Date	4	-77.06	162.3	4.17	0.021
13	Lg Snag Density + Date	3	-78.18	162.5	4.35	0.019
14	Stand Age + Lg Snag Density + Habitat5km + Date	5	-76.13	162.5	4.39	0.019
15	Stand Age x Habitat5km + Date	5	-76.38	163.0	4.89	0.015
16	Stand Age + Lg Snag Density + Date	4	-77.52	163.2	5.09	0.013
17	Stand Age x Lg Snag Density + Habitat5km + Date	6	-75.97	164.3	6.15	0.008
18	Stand Age x Habitat5km + Lg Snag Density + Date	6	-76.12	164.6	6.45	0.007
19	Stand Age x Lg Snag Density	5	-77.52	165.3	7.17	0.005
20	Null	1	-83.28	168.6	10.47	0.001

Table A1.3. Comparison of all generalized linear models used to determine the relationship between Southeastern American Kestrel nest productivity and environmental covariates. We compared models using log-likelihood (LL), Akaike’s Information Criterion corrected for small sample sizes (AICc), and AICc weights. We also report the number of parameters (K) and model differences (Δ AICc). Date is the incubation initiation date. Large (Lg) snag density is snags ≥ 25 cm dbh. Habitat is the amount of early successional sand pine scrub ≤ 15 years old within 5 km of the nest. Nests were located in Ocala National Forest, Florida, USA, and monitored from March to August, 2018–2019.

	Model	K	LL	AICc	Δ AICc	Weight
1	Date	2	-86.99	178.2	0.00	0.256
2	Null	1	-88.65	179.4	1.17	0.143
3	Habitat5km + Date	3	-86.77	180.0	1.80	0.104
4	Snag Density + Date	3	-86.91	180.3	2.08	0.091
5	Lg Snag Density + Date	3	-86.91	180.3	2.09	0.090
6	Stand Age + Date	3	-86.98	180.4	2.23	0.084
7	Habitat5km + Lg Snag Density + Date	4	-86.70	182.2	3.99	0.035
8	Habitat5km + Snag Density + Date	4	-86.72	182.2	4.03	0.034
9	Stand Age + Habitat5km + Date	4	-86.77	182.3	4.13	0.033
10	Stand Age + Snag Density + Date	4	-86.90	182.6	4.39	0.029
11	Stand Age + Lg Snag Density + Date	4	-86.90	182.6	4.40	0.028
12	Stand Age x Habitat5km + Date	5	-86.11	183.4	5.24	0.019
13	Stand Age + Lg Snag Density + Habitat5km + Date	5	-86.69	184.6	6.40	0.010
14	Stand Age + Snag Density + Habitat5km + Date	5	-86.71	184.6	6.44	0.010
15	Stand Age x Lg Snag Density + Date	5	-86.90	185.0	6.81	0.009
16	Stand Age x Snag Density + Date	5	-86.90	185.0	6.82	0.008
17	Stand Age x Habitat5km + Snag Density + Date	6	-86.08	185.9	7.71	0.005
18	Stand Age x Habitat5km + Lg Snag Density + Date	6	-86.11	186.0	7.76	0.005
19	Stand Age x Lg Snag Density + Habitat5km + Date	6	-86.62	187.0	8.80	0.003
20	Stand Age x Snag Density + Habitat5km + Date	6	-86.71	187.2	8.96	0.003

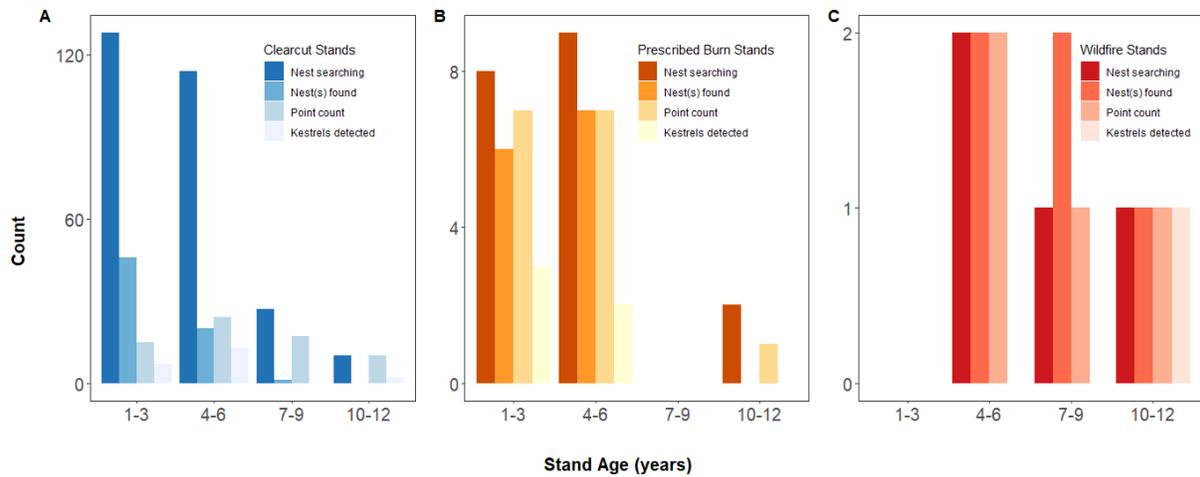


Fig. A1.1. Comparison of counts of stands where nest searching occurred, nests found, stands with point counts, and stands with kestrels detected, grouped by stand age and treatment: A) clearcut, B) prescribed burn (preceded by clearcut), and C) wildfire. All point count and nest searching surveys were conducted during the 2018–2019 breeding seasons in Ocala National Forest, Florida, USA. Stand age is defined as the number of years since the stand was cut or burned. No kestrels were detected in stands >10 years old.