

Nest Defense Behaviors of Native Cavity-Nesting Birds to European Starlings¹

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Abstract

We used behavioral experiments to evaluate competition for nest sites and the extent to which European Starlings (*Sturnus vulgaris*) are seen as a threat by native bird species at the San Joaquin Experimental Range, Madera County, CA. We quantified the level of aggressive behavior of four species of native cavity-nesting birds to starlings at active nests in trees and nest boxes. In 2000, we presented a life-like model of a starling at active nests of native cavity-nesting species, placed in front of the nest opening. In 2001, a House Sparrow (*Passer domesticus*) model was used as a control, with both species presented at nests. Models were mounted on a piece of wood and placed on top of the nest box. Responses were coded as sporadic scolding, continuous scolding, aggressive flight, and attack. Placement of the starling model in front of the cavity elicited a relatively more aggressive response than that elicited by a model placed on top of the nest box. Oak Titmouse (*Baeolophus inornatus*) responses consisted entirely of scolding except for one aggressive flight toward the model, but Western Bluebird (*Sialia mexicana*), Ash-throated Flycatcher (*Myiarchus cinerascens*), and Acorn Woodpecker (*Melanerpes formicivorus*) responses included physical attacks on the starling model. The starling model elicited a significantly stronger response from Oak Titmice and Western Bluebirds than the sparrow model. Although sample sizes were small, Ash-throated Flycatcher responses to the starling model included both aggressive flights and attacks, while neither behavior was seen in response to the sparrow model. Acorn Woodpecker response to the starling model at three nests tested was strong, consisting of attacks on the model by up to seven members of the group. Over the two years of the study, we observed nest usurpation and/or depredation by starlings at seven nests of five species. Our results show that Western Bluebirds, Oak Titmice, Ash-throated Flycatchers, and Acorn Woodpeckers recognize starlings as potential aggressors. We recommend the use of nest boxes to reduce the potential for nest-site competition between starlings and some native cavity-nesting species.

Keywords: Acorn Woodpecker, Ash-throated Flycatcher, cavity-nesting birds, European Starling, nest defense, nest-site competition, Oak Titmouse, *Sturnus vulgaris*, Western Bluebird.

Introduction

The European Starling (*Sturnus vulgaris*) was introduced to North America in 1890, and rapidly spread throughout most of North America (Kessel 1953). Their range in North America now extends from arctic Canada to the subtropics of Mexico (Feare 1984). Between 1968 and 1975, starling numbers increased an average of 16 percent per year (Robbins and Erskine 1975), rendering them one of the most abundant birds in North America. Starlings were first documented in California in 1942 (Jewett

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1942), and are now likely the most abundant Californian bird with numbers estimated in the tens of millions (Small 1994). By 1970, several nesting pairs were documented on the San Joaquin Experimental Range (hereafter SJER), located in the foothills of Madera County (Newman and Duncan 1973). During the last 25 years, starling numbers have increased dramatically at SJER (Purcell and others 2002). Starlings are now abundant nesters in both natural and excavated tree cavities throughout SJER and the foothill oak woodlands of California.

Starlings are aggressive nest competitors, known to evict native species from cavities (van Balen and others 1982, Ingold 1989, Kerpez and Smith 1990, Troetschler 1976) and even kill potential competitors for nest sites (Kessel 1957). Increases in starling abundance are expected to lead to decreased availability of nest cavities for native cavity-nesting species. Other than habitat loss, starlings may be the biggest threat to cavity-nesting birds in oak woodlands in California.

The objective of this study was to assess nest-site competition between European Starlings and native cavity-nesting bird species by examining whether starlings visiting a nest cavity were viewed as a threat by the current occupants of the cavity. We quantified the behavioral response of four species of native cavity-nesting birds to the presence of starlings at the nest site by performing behavioral trials at active nests. We also recorded incidental observations of aggression and nest usurpation by starlings.

Methods

Study Area

This research was conducted at the San Joaquin Experimental Range (hereafter SJER) in the western foothills of the Sierra Nevada, in Madera County, approximately 40 km north of Fresno, CA (*fig. 1*). SJER is 1,875 ha, with an elevation range between 215 and 520 m. The climate at SJER is Mediterranean, with cool, wet winters and hot, dry summers. Mean annual precipitation is 48.6 cm, 95 percent of which falls between October and April.

The vegetation is primarily blue oak foothill pine woodland (Mayer and Laudenslayer 1988) with blue oak (*Quercus douglasii*), interior live oak (*Q. wislizenii*), and foothill pine (*Pinus sabiniana*) as co-dominants. The sparse understory includes wedgeleaf ceanothus (*Ceanothus cuneatus*), chaparral whitethorn (*C. leucodermis*), and Mariposa manzanita (*Arctostaphylos viscida* ssp. *mariposa*). In drier areas, the vegetation is classified as blue oak woodland (Mayer and Laudenslayer 1988) and is dominated by blue oak with a grassland understory. SJER has been lightly to moderately grazed since the early 1900s, except for a 29 ha Research Natural Area that has not been grazed since 1934.

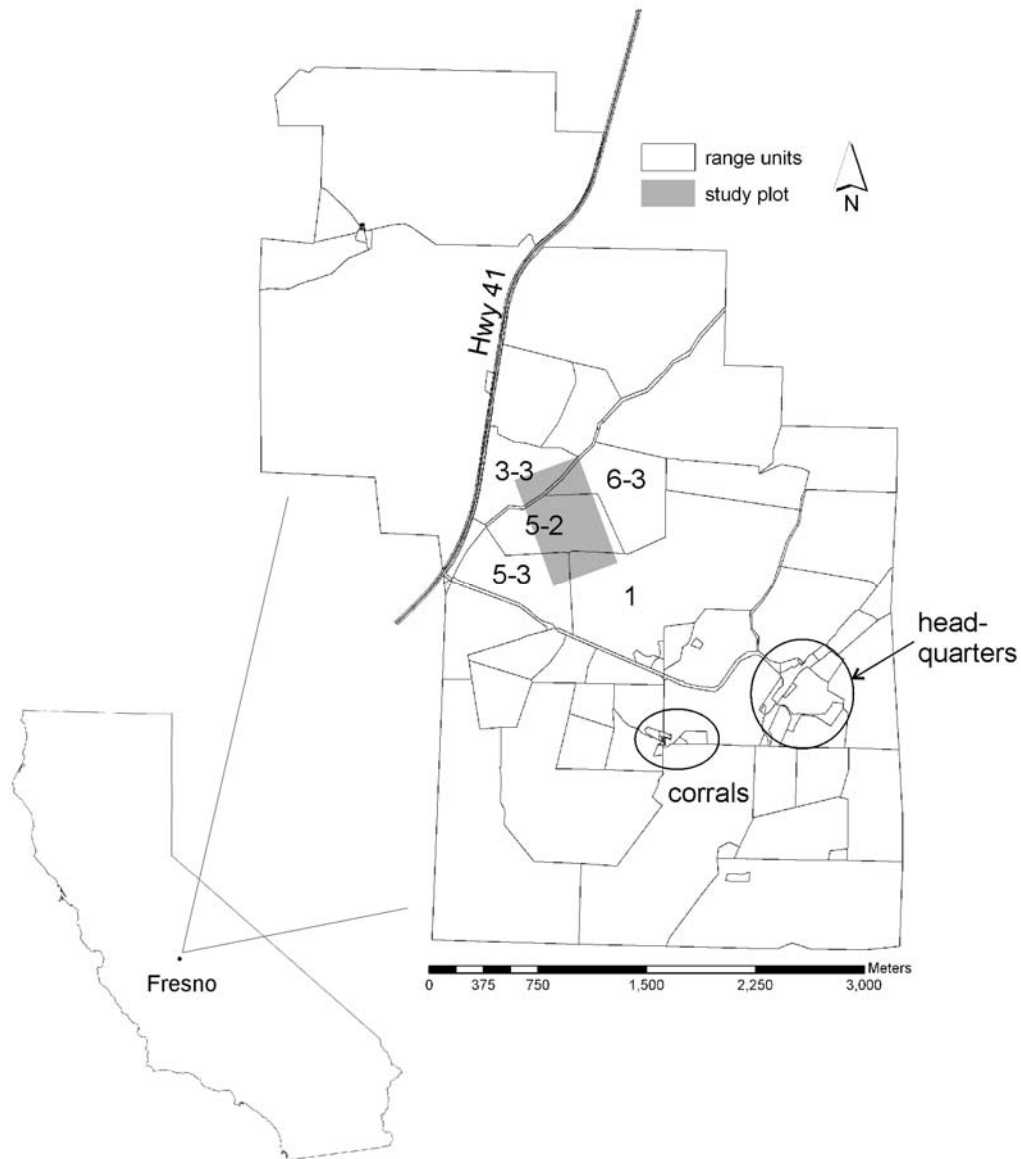


Figure 1—Map of San Joaquin Experimental Range showing range units and study plot.

Fieldwork

The cavity-nesting bird community at SJER includes two species of primary cavity nesters, Acorn Woodpeckers (*Melanerpes formicivorus*) and Nuttall's Woodpeckers (*Picoides nuttalli*), that excavate cavities used to a large degree by secondary cavity nesters. Secondary cavity nesters are particularly diverse in oak woodlands and at SJER, the most abundant of them include Ash-throated Flycatchers (*Myiarchus cinerascens*), Violet-green Swallows (*Tachycineta bicolor*), Oak Titmice (*Baeolophus inornatus*), White-breasted Nuthatches (*Sitta carolinensis*), Bewick's Wrens (*Thryomanes bewickii*), House Wrens (*Troglodytes aedon*), Western Bluebirds (*Sialia mexicana*), and European Starlings.

We located nests of cavity-nesting birds at SJER throughout the 2000 and 2001 breeding seasons. We primarily searched for nests on a 49 ha study plot located in grazed pastures (*fig. 1*), although we also searched for nests in other areas of SJER to increase sample sizes. Nests off the study plot were primarily located along roads accessing different portions of the study area in addition to areas near human habitation in the headquarters area.

In addition to nests in tree cavities, we monitored 59 pairs of nest boxes on the study plot, placed approximately 80 m apart. A pair of redwood nest boxes was randomly placed on major trunks of trees. Each box pair consisted of one box with an entrance diameter of 5.1 cm, and a box with either a 3.8 cm or 3.2 cm opening. Nest boxes with a 5.1 cm opening allowed access by both starlings and native cavity nesters, whereas boxes with smaller entrance diameters excluded starlings. Nest boxes were placed at a height of approximately 2 m.

Nests were examined regularly to determine activity and nesting stage. We used a fiberoptic scope to view the contents of nests in tree cavities in 2000 (Purcell 1997). To access cavities higher than 2 m, extension ladders and various tree climbing methods were used. In 2001, both the fiberoptic scope and a probing videocamera system (TreeTop I, Sandpiper Technologies, Inc.) were used.

We conducted behavioral trials at the nests of four species: Acorn Woodpecker, Ash-throated Flycatcher, Oak Titmouse, and Western Bluebird. We attempted to test responses of nesting birds during the incubation period to control for potential changes in nest defense behavior related to investment in the nest (Biermann and Robertson 1981), but this was not always possible. Of all nests tested, 80 percent were tested during the incubation period with the balance tested during the nestling period. No nests were used more than once to avoid problems of habituation or sensitization (Knight and Temple 1986).

Two types of behavioral trials were carried out to observe the responses of native cavity nesters to potential nest competitors. In 2000, we placed a life-like model of a starling near the entrance of active nests and recorded the behavioral responses of the nesting pair (*fig. 2*). The model was made using a euthanized starling trapped at SJER. The legs were reinforced with a light-gauge wire left projecting from the plantar region for attaching the model. The bird was arranged into a lifelike pose, wrapped in a paper towel, frozen at -80° C, and placed into a Vertis Vacu-station 1SL vacuum dehydrator for approximately 48 hours. The model was mounted on a blue oak branch.



Figure 2—For the 2000 behavioral trials, a European Starling model was positioned in front of the box.

Nests in both tree cavities and nest boxes were used for these trials. For nests in nest boxes, the model was presented by hooking the distal end of the branch under the hanging wire on the nest box. The model was positioned facing the box entrance no more than 0.2 m away (*fig. 2*). To present the model at cavity nests in trees, the model on the oak branch was attached to a telescoping pole and attached to the tree with a bungee cord. The model positioned approximately 0.5 m from the entrance of a nest cavity.

In 2001, we tested the responses of nesting birds to both starlings and a control species. We selected a female House Sparrow (*Passer domesticus*) as the control species for the following reasons. Female House Sparrows are characterized by drab coloration with no distinct markings except for a dull eye stripe. House Sparrows are a non-native species that are rare in oak woodlands outside of human habitation. Although there is evidence for nest-site competition between House Sparrows and Eastern Bluebirds (*Sialia sialia*) (Gowaty 1984), there is limited opportunity for interaction between sparrows and native cavity-nesters at SJER. At SJER they are uncommon and are found around buildings in the headquarters area only. They build nests in cavities, crevices, and shrubs near buildings and their nest sites may not be generally limiting due to the flexibility in nest site use (Stewart 1973). Thus, we assumed that House Sparrows would not be perceived as a threat to native cavity-nesting birds or that any response would provide a conservative test for comparison with starlings. A coin toss determined whether a nest was to be presented with the starling or the sparrow model.

The models were prepared using the same technique as in 2000, except they were mounted on a piece of wood the same dimensions as the roofs of the nest boxes. Models were presented at the nest by placing the mount on top of the box with the head of the model placed directly above the box entrance (*figs. 3, 4*).

In both years, discreet observations were made of the activities of the nesting pair, prior to each test. If either member of the pair detected the observer during setup, the attempt was abandoned and no further trials were performed at that nest. When models were successfully deployed without detection, observations were made from an area of either suitable natural cover or a camouflage blind. Camouflage clothing was worn to reduce the chance of detection.



Figure 3—For the 2001 behavioral trials, a European Starling model was placed on top of the box.



Figure 4—A House Sparrow model placed on top of the box following the 2001 protocol.

The placement of the models for the 2001 breeding season was altered to decrease the chance of being detected by the nesting pair during setup. The 2000 season setup required several minutes at the nest to position the model correctly. On a few occasions we were detected by the nesting pair during the setup, obliging us to terminate the trial and exclude the nest from further trials. Placing the model on top of the nest box greatly decreased the time spent at the nest and the likelihood of detection by the pair. Consequently, only nests in nest boxes were tested in 2001.

In both years, observations were made for 3 minutes beginning when one member of the breeding pair acknowledged the model. Initial observations indicated a 3-minute trial was sufficient to observe the maximum response. Acknowledgment of the model was usually signaled by a change in the behavior of the bird. This could include a switch from foraging to posturing, a change from a foraging call to a scold, or physical aggression toward the model. We recorded two potential types of behavior during each trial—scolding and physical approach. Scolding was scored as sporadic or continuous. Sporadic scolding was defined as scolding for no more than a total of 1.5 minutes of the 3-minute observation. Continuous scolding lasted more than 1.5 minutes of the observation. Physical approach to the model was scored as aggressive flight or attack. Aggressive flight was defined as a deliberate flight toward the model within a 1 m radius of the model. Attack was defined as physical contact with the model. We also estimated the shortest distance between the nest occupant(s) and the model, and recorded whether either occupant entered the cavity during the trial.

Incidental observations of aggression associated with nest usurpation were recorded for all cavity-nesting species, both on and off of the study plot in the course of field activities. We attempted to identify the aggressor, subordinate, and victor species, as well as the nature and location of the interaction.

Statistical Analysis

We tallied the observations in each behavioral category by species, year, and model. For 2001, the numbers of each behavior observed in response to the starling and sparrow models were compared using a generalization of Fisher's exact test (Zar 1974) for Oak Titmouse and Western Bluebird. We set alpha equal to 0.10 due to small sample sizes and the low power of contingency table tests. For Oak Titmouse, we looked at only scolding behaviors (none, sporadic, and continuous) due to the small number of observations involving physical approach. For Western Bluebird, we examined both the scolding and physical approach variables. We compared responses to just the starling model in 2000 and 2001 to see if there was a differential effect of placing the model in front of the nest vs. on top of the nest box for Oak Titmouse (scolding only) and Western Bluebird (scolding and physical approach).

Results

Behavioral Trials

A total of 65 nests of the four species of native-cavity nesting birds tested in behavioral trials were located in tree cavities during the two years of the study. Three of the study species made an additional 117 nesting attempts in nest boxes. Acorn Woodpeckers did not use nest boxes, nor did European Starlings. Although starlings readily use nest boxes in other areas, they have not been observed to use them at SJER.

Oak Titmouse response to models consisted almost entirely of scolding, either sporadic or continuous. On only one occasion did a titmouse react with an aggressive flight toward the model, and no physical attacks on the model were observed. In 2000, behavioral trials were done at 17 Oak Titmouse nests using the starling model looking into the cavity. Titmouse scolding was sporadic at 24 percent of the nests and continuous at 76 percent of the nests tested (*table 1*). Based on only the scolding categories in 2001, the starling model elicited a stronger response than the sparrow model ($\chi^2 = 6.01$, $df = 2$, $P = 0.047$). Response to the starling model did not differ between years when the placement of the starling model was changed ($\chi^2 = 0.01$, $df = 1$, $P = 1.00$).

Table 1—Oak Titmouse behavioral response to models of European Starlings (Starling) and House Sparrows (Sparrow) at nests, including the number of trials resulting in sporadic or continuous scolding, aggressive flight or attack, the number of trials where the occupants entered the nest, and the average approach distance to the model.

Year	Model	2000	2001	
		Starling (N = 17)	Starling (N = 12)	Sparrow (N = 10)
Scolding	Sporadic	4	3	4
	Continuous	13	9	3
Aggressive Flight		1	0	0
Attack		0	0	0
Entered cavity		4	4	4
Distance to model (cm)		75	88	151

Response of Western Bluebirds varied from sporadic scolding to attack (*table 2*). In 2000, behavioral trials were done at 13 bluebird nests. Scolding was scored as sporadic at 8 percent of the nests and was continuous at 31 percent, with no scolding noted at 17 percent of nests (*table 2*). Scolding may have been underestimated due to the distance from which the observations were made and the faint nature of Western Bluebird's call and scold notes. Aggressive flight was observed in 8 percent of the trials and physical attacks were observed in 77 percent. Physical attacks were fierce, sometimes involved both members of the pair, and included landing on the model, biting, and attempting to peck the eyes. Bluebirds went to the nest 15 percent of the time. In 2001, the only response to the sparrow model was sporadic scolding at two of the eight nests tested. Nest occupants presented with the starling model responded with aggressive flights in 43 percent of the trials and physically attacked the model in 14 percent of the trials (*table 2*). Response to the starling and sparrow models did not differ for the scolding variable ($\chi^2 = 3.61$, $df = 2$, $P = 0.184$), but bluebirds showed a significantly stronger physical approach response to the starling compared to the sparrow model ($\chi^2 = 5.33$, $df = 2$, $P = 0.077$). Bluebirds went to the nest 43 percent of the time when the starling model was used but always entered the nest when the sparrow model was used. Bluebirds responded more strongly to the starling model placed in front of the nest in 2000, compared to the model placed on top of the nest box 2001 in terms of both scolding ($\chi^2 = 5.93$, $df = 2$, $P = 0.090$) and physical approach ($\chi^2 = 7.43$, $df = 2$, $P = 0.023$).

Table 2—Western Bluebird behavioral response to models of European Starlings (Starling) and House Sparrows (Sparrow) at nests, including the number of trials resulting in sporadic or continuous scolding, aggressive flight, and attack, the number of trials in which the occupant entered the nest, and the average approach distance to the model.

Year Model	2000		2001	
	Starling (N = 13)	Starling (N = 7)	Sparrow (N = 8)	
Scolding	Sporadic	1	4	2
	Continuous	4	1	0
Aggressive Flight	1	3	0	
Attack	10	1	0	
Entered cavity	2	3	8	
Distance to model (cm)	55	106	10	

Sample sizes for Ash-throated Flycatcher trials were low due to low nest numbers for this species coupled with the fact that they are sit and wait predators that can remain observant of the nest while foraging, increasing the incidence of detection during the set up. Both aggressive flights and physical attacks were observed in response to the starling model, but response to the sparrow model was limited to sporadic scolding (*table 3*).

Table 3—Ash-throated Flycatcher behavioral response to models of European Starlings (Starling) and House Sparrows (Sparrow) at nests, including the number of trials resulting in sporadic or continuous scolding, aggressive flight, and attack, the number of trials in which the occupant entered the nest, and the average approach distance of the occupant to the nest.

Year		2000	2001	
Model		Starling (N = 1)	Starling (N = 2)	Sparrow (N = 3)
Scolding	Sporadic	0	1	2
	Continuous	1	1	0
Aggressive Flight		0	1	0
Attack		1	1	0
Entered cavity		0	2	1
Distance to model (cm)		10	10	07

Acorn Woodpecker response was strong to the three trials performed on Acorn Woodpecker nests in 2000. In all three cases, one individual initiated the attack by making an alarm call and then flew in and attacked the model. This was followed by subsequent attacks on the model by other members of the group. Scolding and attacks were continuous throughout the observations. In two of the trials, there were at least seven woodpeckers involved in attacks on the model.

Nest Usurpation and Other Observations

In 2000, four nest usurpations of active nests by starlings were observed. An Oak Titmouse nest was usurped during the nest-building stage and occupied by a starling pair. The displaced titmouse re-nested in the same tree in another cavity with a smaller entrance. Both nests successfully fledged young. Two Western Bluebird nests were usurped, both during the building stage. In one case, bluebirds were observed bringing nest material into a cavity which starlings later occupied. At another cavity in a telephone pole, we observed fierce interactions between starlings and bluebirds over the cavity, including a male and female bluebird attacking and fighting to the ground a starling as it approached the nest. In subsequent days, we observed a starling intercepting the female bluebird and making physical contact as she made trips. The female bluebird was later found dead at the base of the pole. The starlings nested in the contested cavity. An active Ash-throated Flycatcher nest was usurped during the laying or incubation stage. When the cavity was checked, the clutch of three eggs noted on the previous visit was gone. A pair of flycatchers was observed at the nest but left the area after a pair of starlings entered the nest cavity. The starlings subsequently nested in the usurped cavity. It should be noted that three of the four usurpations observed in 2000 took place in nests located in the vicinity of human habitation and associated livestock corrals, where starling densities appear to be highest.

In 2001, three nest usurpations by starlings were recorded. We observed a White-breasted Nuthatch entering a cavity used by nuthatches the previous year and removing old material. Starlings occupied the cavity shortly after this observation. The same Oak Titmouse nest usurped in 2000 was also usurped by starlings in 2001. In this case, the titmouse did not re-nest in the same tree. We observed a starling inside an Acorn Woodpecker nest cavity that had contained four eggs on the previous

visit. The woodpecker was calling aggressively. When the starling flew from the cavity, the woodpecker made an aggressive flight toward it. When checked, the nest was empty and eggshell fragments were found below the nest. As the starling did not nest in the usurped cavity, this appears to be a depredation event. Finally, at a Western Bluebird nest with three eggs, a starling was seen at the nest entrance after the nest was depredated. We lack evidence in this case to call it usurpation and there was no direct evidence that a starling was responsible for depredating the nest.

Other field observations of interactions between starlings and native species included Acorn Woodpeckers chasing starlings (one case) and starlings displacing Acorn Woodpeckers (three cases).

Discussion

One of the strongest arguments for competition is when aggression occurs over a limiting resource (Wiens 1989). Results of behavioral experiments and field observations in this study provide convincing evidence for competition between European Starlings and native cavity-nesting species at SJER. Data from behavioral experiments clearly show that Acorn Woodpeckers, Ash-throated Flycatchers, Western Bluebirds, and Oak Titmice recognized starlings as potential aggressors. Acorn Woodpeckers and Western Bluebirds reacted most strongly to starling models. Field observations of usurpations and direct aggression are indicative of interference competition between starlings and these four species and White-breasted Nuthatches.

An alternate interpretation of the nest defense behaviors observed here is that the behaviors observed were intended to repel predators rather than nest-site competitors. While we believe that the data from this study and others that have shown nest defense responses to starlings are most readily interpreted as resulting from competition for nest sites (e.g., Dobkin and others 1995, Ingold 1989, 1994, Kerpez and Smith 1990, Troetschler 1976, Weitzel 1988, Wiebe 2003), we are intrigued by the idea that European Starlings are nest predators as well. We recorded indirect evidence of mortality of an adult female Western Bluebird at a usurped nest. Direct mortality of adult birds of other species as well as conspecifics by starlings has been previously documented (Kessel 1957). In addition, we noted depredation of eggs by starlings on two occasions; in one case the starlings did not subsequently occupy the nest cavity. If starlings are nest predators, starlings may be further impacting native species by directly reducing their reproductive success. This question deserves further study.

Secondary cavity-nesting species are diverse and abundant at SJER. They are largely dependent on primary cavity nesters for nest sites and are potentially highly vulnerable to lowered availability of nest cavities, which are generally assumed to be limiting (Brush 1983, Cline and others 1980, Stauffer and Best 1982). An additional potentially aggravating factor related to nest-site limitation is the poor nest sanitation habits of starlings, which may render nests unusable to later nesting species (Feare 1984). Nevertheless, Acorn Woodpeckers also perceived starlings as a threat. We observed a strong reaction to starlings at nest sites and usurpation of Acorn Woodpecker nests by starlings, suggesting they are negatively impacted by starlings at SJER.

Western bluebirds overwhelmingly used nest boxes where they were available and may have shifted to nest boxes to reduce competition for nest cavities in trees. It

is interesting to note that three of the five bluebird nests found in trees and poles were usurped by starlings during the two years of this study, and all bluebird nests not in nest boxes failed.

Starlings were most abundant around human habitation and high-density livestock areas at SJER, and the majority of random aggressive interactions between starlings and native cavity nesters took place in these areas. The high numbers of starlings in these areas may have increased the probability of interactions between starlings and native species, and the high incidence of aggression may be reflective of high starling densities rather than simply a lack of nest sites. On the other hand, high starling numbers and the relatively high starling nest densities in these areas likely constrain available nest sites for native species leading to competitive interactions over nest sites. Few direct incidences of direct aggression, aside from those elicited during behavioral trials, were observed on the study plot where starling densities were lower, even though much more time was spent on the study plot relative to time spent in other areas. In addition, the presence of nest boxes on the study plot may have reduced nest-site competition relative to areas without boxes.

Because energetic costs and physical risks related to aggression may be high, opponents should try to minimize risk through the suppression, reduction, or redirection of an attack (Moynihan 1998). For bluebirds, placement of the starling model in front of the nest box opening facing into the cavity elicited a more aggressive response than that elicited when the model was placed on top of the box. With the starling model on top of the box, bluebirds would often perch in a nearby tree and watch the model from above rather than attacking it as was the case when the model was in front of the cavity. In these cases, the bluebird may have been evaluating the necessity of aggression based on the location of the model. With the model on top of the box, the threat may not appear as immediate as the potential competitor may not have discovered the nest, reducing the possibility of depredation (Burhans 2000). Bluebirds detecting the model in front of the cavity appeared to perceive an immediate threat and acted more aggressively. In most cases, bluebirds reacted by physically attacking the model. These attacks were surprisingly intense and violent.

We expect more aggressive defense of nests by larger species. Although starlings are only slightly larger than Acorn Woodpeckers, they are roughly three times larger, in terms of mass, than Western Bluebirds and Ash-throated Flycatchers, and nearly five times heavier than Oak Titmice. The response levels noted in this study roughly correlate with body size. We noted the most violent response to starlings at nests by Acorn Woodpeckers and Western Bluebirds. Responses of the smaller Oak Titmice were limited to scolding.

The invasion of non-native species, coupled with habitat loss, may have significant harmful effects on the diversity and abundance of native species. We recommend further study of methods for reducing the impacts of European Starlings on native cavity-nesting birds. Previous work done at SJER indicated that starlings avoided ungrazed pastures and areas with deep litter (Purcell and others 2002). Research on the effects of litter depth and grass height could yield recommendations on grazing intensity and mowing practices that could help reduce starling numbers and their impacts on native bird species of California's oak woodlands. In areas where cavities are limiting, we recommend the use of nest boxes to reduce competition for nest sites. Nest boxes should have entrance diameters small enough

to exclude starlings and should be monitored regularly to ensure that the openings have not been enlarged by woodpeckers, allowing access to starlings.

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References

- Biermann, G.C.; Robertson, R.J. 1981. **An increase in parental investment during the breeding season.** *Animal Behavior* 29:487-489
- Brush, T. 1983. **Cavity use by secondary cavity-nesting birds and response to manipulations.** *Condor* 85:461-466.
- Burhans, D.E. 2000. **Avoiding the nest: responses of field sparrows to the threat of predation.** *Auk* 117:803-806.
- Cline, S.P.; Berg, A.B.; Wight, H.M. 1980. **Snag characteristics and dynamics in Douglas-fir forests, western Oregon.** *Journal of Wildlife Management* 44:773-86.
- Dobkin, D.S.; Rich, A.C.; Pretare, J.A.; Pyle, W.H. 1995. **Nest-site relationships among cavity-nesting birds of riparian and snow-pocket aspen woodlands in the northwestern Great Basin.** *Condor* 97:694-707.
- Feare, C. 1984. **The Starling.** New York: Oxford University Press; 24 p.
- Gowaty, P.A. 1984. **House Sparrows kill Eastern Bluebirds.** *Journal of Field Ornithology* 55:378-380.
- Ingold, D.J. 1989. **Nesting phenology and competition for nest sites among Red-headed and Red-bellied Woodpeckers and European Starlings.** *Auk* 106: 209-217.
- Ingold, D.J. 1994. **Influence of nest-site competition between European Starlings and woodpeckers.** *Wilson Bulletin* 106:227-241.
- Jewett, S.G. 1942. **The European Starling in California.** *Condor* 44:79.
- Kerpez, T.A.; Smith, N.S. 1990. **Competition between European Starlings and native woodpeckers for nest-cavities in Sagueros.** *Auk* 107:367-375.
- Kessel, B. 1953. **Distribution and migration of the European Starling in North America.** *Condor* 55:49-67.
- Kessel, B. 1957. **A study of the breeding biology of the European Starling (*Sturnus vulgaris*) in North America.** *American Midland Naturalist* 58:257-331.
- Knight, R.L.; Temple, S.A. 1986. **Why does intensity of avian nest defense increase during the nesting cycle?** *Auk* 103:318-327.
- Mayer, K.E.; Laudenslayer, W.F. 1988. **A guide to wildlife habitats of California.** California Department of Forestry and Fire, Sacramento, CA, USA; 166 p.

- Moynihan, M. 1998. **The social regulation of competition and aggression in animals.** Washington, D.C.; Smithsonian Institution Press; 158 p.
- Newman, T.F.; Duncan, D.A. 1973. **Vertebrate fauna of the San Joaquin Experimental Range, California: a checklist.** Gen. Tech. Rep. PSW-GTR-6. Berkeley, CA: Pacific Southwest Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture; 21 p.
- Purcell, K.L. 1997. **Use of a fiberscope for examining cavity nests.** Journal of Field Ornithology 68:283-286.
- Purcell, K.L.; Verner, J.; Mori, S.R. 2002. **Factors affecting the abundance and distribution of European Starlings (*Sturnus vulgaris*) at the San Joaquin Experimental Range.** In: Standiford, R.B.; McCreary, D.D.; Purcell, K.L., technical coordinators. Proceedings of the fifth symposium on oak woodlands: oaks in California's changing landscape. 2001 October 22-25; San Diego, CA. Gen. Tech. Rep. PSW-GTR-184. Albany, CA: Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture; 305-321.
- Robbins, C.S.; Erskine, A.J. 1975. **Population trends in nongame birds in North America.** Transactions of the North American Wildlife and Natural Resource Conference 40:288-293.
- Small, A.S. 1994. **California birds, their status and distribution.** Vista, CA: Ibis Publishing Company; 342 p.
- Stauffer, D.F.; Best, L.B. 1982. **Nest-site selection by cavity-nesting birds of riparian habitats in Iowa.** Wilson Bulletin 94:329-337.
- Stewart, P.A. 1973. **Replacement of cavity-hunting starlings and house sparrows after removal.** Wilson Bulletin 85:291-294.
- Troetschler, R.G. 1976. **Acorn Woodpecker breeding strategy as affected by starling nest-hole competition.** Condor 78:151-165.
- van Balen, J.H.; Booy, C.J.; van Franeker, J.A.; Osieck, E.R. 1982. **Studies on hole nesting birds in natural nest sites.** Ardea 70:1-24.
- Weitzel, N.H. 1988. **Nest-site competition between the European Starling and native breeding birds in northwestern Nevada.** Condor 90:515-517.
- Wiebe, K.L. 2003. **Delayed timing as a strategy to avoid nest-site competition: testing a model using data from starlings and flickers.** Oikos 100:291-298.
- Wiens, J.A. 1989. **The ecology of bird communities. Vol. 2.** Cambridge University Press, Cambridge. 316 p.
- Zar, J.H. 1974. **Biostatistical analysis.** Englewood Cliffs, NJ: Prentice-Hall, Inc. 620 p.

- Moynihan, M. 1998. **The social regulation of competition and aggression in animals.** Washington, D.C.; Smithsonian Institution Press; 158 p.
- Newman, T.F.; Duncan, D.A. 1973. **Vertebrate fauna of the San Joaquin Experimental Range, California: a checklist.** Gen. Tech. Rep. PSW-GTR-6. Berkeley, CA: Pacific Southwest Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture; 21 p.
- Purcell, K.L. 1997. **Use of a fiberscope for examining cavity nests.** Journal of Field Ornithology 68:283-286.
- Purcell, K.L.; Verner, J.; Mori, S.R. 2002. **Factors affecting the abundance and distribution of European Starlings (*Sturnus vulgaris*) at the San Joaquin Experimental Range.** In: Standiford, R.B.; McCreary, D.D.; Purcell, K.L., technical coordinators. Proceedings of the fifth symposium on oak woodlands: oaks in California's changing landscape. 2001 October 22-25; San Diego, CA. Gen. Tech. Rep. PSW-GTR-184. Albany, CA: Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture; 305-321.
- Robbins, C.S.; Erskine, A.J. 1975. **Population trends in nongame birds in North America.** Transactions of the North American Wildlife and Natural Resource Conference 40:288-293.
- Small, A.S. 1994. **California birds, their status and distribution.** Vista, CA: Ibis Publishing Company; 342 p.
- Stauffer, D.F.; Best, L.B. 1982. **Nest-site selection by cavity-nesting birds of riparian habitats in Iowa.** Wilson Bulletin 94:329-337.
- Stewart, P.A. 1973. **Replacement of cavity-hunting starlings and house sparrows after removal.** Wilson Bulletin 85:291-294.
- Troetschler, R.G. 1976. **Acorn Woodpecker breeding strategy as affected by starling nest-hole competition.** Condor 78:151-165.
- van Balen, J.H.; Booy, C.J.; van Franeker, J.A.; Osieck, E.R. 1982. **Studies on hole nesting birds in natural nest sites.** Ardea 70:1-24.
- Weitzel, N.H. 1988. **Nest-site competition between the European Starling and native breeding birds in northwestern Nevada.** Condor 90:515-517.
- Wiebe, K.L. 2003. **Delayed timing as a strategy to avoid nest-site competition: testing a model using data from starlings and flickers.** Oikos 100:291-298.
- Wiens, J.A. 1989. **The ecology of bird communities. Vol. 2.** Cambridge University Press, Cambridge. 316 p.
- Zar, J.H. 1974. **Biostatistical analysis.** Englewood Cliffs, NJ: Prentice-Hall, Inc. 620 p.

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