

**COOPERATIVE NEST DEFENSE BY EUROPEAN STARLINGS (*STURNUS VULGARIS*)
DURING A PREDATORY THREAT**

by

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ABSTRACT

COOPERATIVE NEST DEFENSE BY EUROPEAN STARLINGS (*STURNUS VULGARIS*) DURING A PREDATORY THREAT

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One direct benefit of mating outside the pair bond for female passerine birds is to enlist the aid of neighboring males in communal activities such as nest defense. Female passerines are expected to be more heavily invested in offspring than males. The cooperative neighborhood hypothesis indicates that males will participate in communal nest defense for the public good as they may have sired offspring in neighboring nests. European starlings (*Sturnus vulgaris*) have unique reproductive strategies with not only males producing genetic offspring outside the pair bond in other nests (extra-pair paternity), but females as well (quasi-parasitism, intraspecific brood parasitism). Therefore, I predicted that both males and females would respond to a predation threat in neighboring nests. European starlings were exposed to a taxidermy mount of a Red squirrel (*Tamiasciurus hudsonicus*) (experimental treatment) as well as to a similarly sized/shaped rock (control) on the 11-13th day of the nestling period (day 0 is hatch day). An aggregate score of defensive responses (number of; birds, alarm calls and chips, hits and fly-bys to the nest box) was calculated. Significantly extra birds responded to the experimental than control treatment, demonstrating that the taxidermy mount was effective, and that communal defense occurs in this species. Both male and female European starlings participated in mobbing at neighboring nests during the experimental treatment, supporting one of the main predictions of the cooperative neighborhood hypothesis. Therefore, given the mating system of European starlings, it is likely that parental uncertainty in neighboring nests may increase communal nest defense in this species.

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INTRODUCTION

Variation in Parental Investment

Differences in parental investment are evident across every taxon. On average, females are more invested in their offspring than males (Clutton-Brock, 1991; Queller, 1997; Kokko & Jennions, 2012). In passerine birds, males incubate eggs and provision nestlings less often than do females (Kluyver, 1933; Feare, 1984;). Several hypotheses have been proposed to explain why females generally invest more in their offspring than males (reviewed by Queller, 1997). Understanding the mating system of an avian species may help to distinguish why one sex may spend more time than the other caring for the nestlings.

In birds that are socially monogamous, males will provide paternal care if the nestlings require both parents to be invested for their survival (Emlen & Oring, 1977; Smith, 1977). Male passerines provide care to the offspring of their social mate, but also engage in extra-pair copulations (EPCs) with other females, and sire extra-pair young whom they do not provision (Trivers, 1972; Eliassen & Jorgensen, 2014; Griffith et al., 2002).

Though the benefits for a socially monogamous male engaging in EPCs are clear, there are both advantages and disadvantages to females engaging in copulations outside of the social pair. Some of these advantages include controlling the occurrence and frequency of extra-pair copulations (Lifjeld et al., 1992; Gray, 1996) as well as increasing the genetic quality (Smith, 1988; Otter et al., 1994) or diversity (Gavin & Bollinger, 1985) of their offspring, insuring against the potential infertility of their mate (Simmons, 1990), searching for potential future pair bonds

(Colwell & Oring, 1989; Wagner, 1991; Ens, 1992; Heg et al., 1993), or securing more male parental care through communal nest defense (Stacey, 1982; Davies, 1985).

One potential disadvantage for females engaging in EPCs is decreased parental care from the social mate as the paternity level decreases within the nest (Trivers, 1972; Gladstone, 1979; Queller, 1997). It can therefore be hypothesized that there may be a threshold (Whittingham et al., 1992), as to when a male will retract a portion or all of his paternal care if his paternity becomes too low (Davies, 1992).

When females engage in EPCs, it is most often with nearby neighbors, (Bjorklund & Westman, 1983; Buitron, 1983; Payne, 1983; Gibbs et al., 1990; Westneat, 1993). Doing so may be advantageous to females as it increases paternity uncertainty amongst neighboring males, and results in an increased probability of males assisting with communal nest defense against a potential predator (the cooperative neighborhood hypothesis; Eliassen & Jorgensen, 2014).

Breeding birds have been documented to participate in communal nest defense tactics (Arroyo et al., 2001; Lima, 2009), which include increased vigilance (Lima & Dill, 1990), alarm calls (Trivers, 1971), mobbing (Curio, 1978) and expulsion of intruders (Eliassen & Jorgensen, 2014), allowing females to benefit from the increased paternal protection to their offspring. This defensive attention is often overlooked as a form of parental care since it involves investment toward the public good and is done away from the social nest. However, as long as cooperative behaviours benefit potential offspring and are costly to the male they should be included in reproductive investment (Stacey, 1982; Eliassen & Jorgensen, 2014).

Alarm calling and mobbing when done singly become dangerous (Curio, 1978) and

give away the individual's location (Smith, 1965), making communal defense more efficient when done as a group so all birds can reap the benefits and minimize the costs (Eliassen & Jorgensen, 2014). Eliassen & Jorgensen (2014) predicted that while males are cooperating towards the public good due to the potential of having genetic offspring in these nests, females would be more likely to stay only at their own nest due to maternity certainty (they have no offspring in other nests), and not participate in communal nest defense.

The European starling, *Sturnus vulgaris*, is a semi-colonial breeding passerine that nests in holes and cavities (Feare, 1984; Pinxten et al., 1989 b). They are known as socially monogamous breeders but approximately 20-40% of males are facultatively polygynous (Pinxten et al., 1989 a,b). When both parents provide offspring care, males help with incubating eggs and feeding nestlings (Pinxten et al., 1993 a; Smith et al., 1995; Sandell et al., 1996). Females obtain EPCs (Smith & von Schantz, 1993), therefore males can be uncertain of their genetic paternity within the social nest. Maternity uncertainty also exists in this species due to intraspecific brood parasitism whereby females lay eggs in conspecific neighbouring nests (Yom-Tov et al., 1974; Pinxten et al., 1993 b; Sandell & Diemer, 1999). Quasi-parasitism also occurs; this is a strategy whereby a female obtains EPCs and then lays her egg in the nest of the male who fertilized it (Barber et al. unpublished data). Therefore, the nestling is genetically related to the male but not the female of that nestbox (Griffith et al., 2004; Otter et al., 2011). Because of this diverse mating system, I hypothesize that both males and females will be involved in collective nest defense when faced

with a natural predator at a neighboring nest, as paternity and maternity may be spread across the neighborhood.

Adults typically have two broods a year. Nestlings require parental care during the 21-23 day period following hatching and both parents typically provide care to the nestlings (Feare, 1984). However, one sex can do so singly if the other parent deserts, but fledging success is reduced (Best & Stauffer, 1980). A reduction of care can happen by either the male or the female, leaving the opposite sex to raise the nestlings alone (Trivers, 1972; Smith, 1977; Richmond, 1978; Gowaty, 1983; Hannon, 1984; Martin, 1984; Martin et al., 1985).

The purpose of this research was to determine if the unique mating system from the addition of quasi and intra-specific brood parasitism from females as well as EPCs from both sexes of European starlings would influence collective nest defense when faced with the threat of a natural predator. First, I needed to determine that the natural predator I presented to elicit the nest defense response was effective. It consisted of a taxidermy Red squirrel, *Tamiasciurus hudsonicus*, which was placed on the nestbox (experimental trial); Red squirrels are a predator to eggs and nestlings (Sieving & Wilson, 1998; Bayne & Hobson, 2002). I predicted that more birds would be present during the experimental trial than the control trial (a similar sized and shaped rock placed on the nestbox) to help in communal nest defense. I also predicted there would be increased nest defense by parents and/or other enlistees in the experimental compared to the control trials, as the birds would recognize the squirrel mount as a threat. I also predicted that single birds (no social

mate) would have a lower aggregate score than paired birds due to the decreased response from only one parent and not two.

Though paternity and maternity of nestlings were not determined in this study, the cooperative neighborhood hypothesis predicts that males would help defend conspecific nests because of paternity uncertainty. I predicted that female European starlings would also help in communal nest defense as they might have young in conspecific nests from intraspecific and quasi-brood parasitism. Finally, I predicted that an increased aggregate score would be positively correlated with the 1) total number of provisioning visits and 2) reproductive success (number and proportion of nestlings that fledged) because defense of the nest may be a good indicator of the adults' ability to care for and successfully fledge nestlings (Kleindorfer et al., 2003).

METHODS

Field Work

This study was conducted on the campus of Saint Mary's University, located on 32 hectares of land in the south end of Halifax, Nova Scotia, Canada (44° 37' 54.07" N, 63° 34' 47.09" W) from May through July 2015. Adult European starlings (*Sturnus vulgaris*) were studied in eleven nest boxes over the first brood (from May 15th to 26th) and five nest boxes over the second brood (from June 30th to July 5th). Every nest was checked daily during the laying period and then again daily two days prior to the expected hatch date.

Adults were caught using a simple nest box trap (Stutchbury & Robertson, 1986) and then sexed (Kessel, 1951). Adults that had not been previously caught were given a unique band combination made up of two colored band on their left tarsus and a single colored band on their right tarsus (to identify their sex). In addition, birds were banded with a Canadian Wildlife Service band on their right tarsus.

All 16 nest boxes were observed on the 7-8th and 13-14th day of the nestling period (day 0 is hatch day). Observations were not recorded on days when the weather might have compromised the bird's ability to feed (e.g. very stormy days). Provisioning watches were conducted over a one-hour time period, between the hours of 0700 and 1100. The number of feeding trips made by each parent (sex) to their offspring was recorded. Band combinations of the parents were confirmed at this time. Observers were out of the parents' immediate field of view and sat at least 7.5 meters away.

Experiment

Models were presented to parents of these 16 nest boxes during the 11-13th day of their nestling period. Two models were presented on consecutive days: a taxidermy mount of a Red squirrel (experimental treatment), and a rock that was similar in shape, size and colouring to the squirrel (control treatment). Both model presentations were conducted on each nest box. The order of treatment presentation to each nest box was randomly assigned by flipping a coin. The model was then placed on top of the nest box, approximately 12.7 cm vertically from the hole when the adults were absent. Four black pushpins were used to secure the object so that it would not fall off the angled roof.

All trials occurred between 0830 and 1330. The two trials for each nest box were conducted between 24 and 48 hours apart of each other, and were recorded with a digital camera. Each trial began when the first parent returned to the nest box and continued for a total of three minutes. Observers remained out of the birds' view.

In the event that two closely neighboring nest boxes were tested on the same day, the control trial was conducted first at one of the boxes. If each of the two nest boxes had been assigned an experimental treatment through the coin toss, the trial at the second nest box was delayed for a few hours in order to ensure that the Starlings did not feel threatened for a prolonged amount of time.

The type of observations that were recorded during the trials were chosen based on previous avian studies presenting taxidermy mounts (e.g. Neudorf & Sealy, 1992). These were: 1) date, time and age of nestlings 2) number of adults present

including parents, 3) band combinations (if any) of participating adults, 4) sex of adults, 5) number of hits made to the model (Blancher & Robertson, 1982), 6) number of dives at the model (Blancher & Robertson, 1982), 7) number of fly-bys (flying within approximately 0.5 meters of the model, but no attacks or dives; (Blancher & Robertson, 1982; Neudorf & Sealy, 1992)), 8) number of alarm calls (Blancher & Robertson, 1982), and chips, and 9) any additional observations on behaviors. Band combinations permitted identification of all adults present around the focal nestbox; 27 females and 20 males had been banded at a total of 39 active nestboxes on campus.

Statistical Analysis

Nest defense was quantified using aggregate scores that were the sum of defensive strategies (Smith et al., 1984), which consisted of the total number of: a) birds involved, b) dives at the model or nestbox, c) hits to model or nestbox, d) fly-bys and e) alarm calls and chips (Blancher & Robertson, 1982; Neudorf & Sealy, 1992). All defensive strategies were added for a total resulting in a numerical value. The value was tightly correlated with the intensity of the trial.

All data were tested for normality. Parametric tests were used on normally distributed data while non-parametric tests were used when the data had a non-normal distribution. Graph Pad Prism 5 (San Diego) was used to analyze the data.

Parental social reproductive success was calculated as the number and proportion of nestlings that fledged. As no difference was detected in the total number of visits made to the nestbox by provisioning parents on days 7-8 vs. days 13-14 (paired $t = 0.3567$, $df = 15$ and $P = 0.73$), an average of the two was calculated for

each nestbox. All tests are two-tailed. Results were considered significant when $P \leq 0.05$.

RESULTS

Experimental vs. control trial

Significantly more birds flew to the focal nestbox during the experimental trial compared to the control trial (Wilcoxon $W=45$, $n=16$, $P=0.004$; Figure 1). Aggregate scores in response to the Red squirrel were significantly higher than those to the rock (Wilcoxon $W=136$, $n=16$, $P < 0.0001$; Figure 2).

Males vs. females

In cases where only one parent of a pair flew to the nestbox in response to the model presentation, it was typically the female who did so (a minimum of 5/7 times for the control and a minimum of 5/8 times for the experimental).

Paired vs. unpaired

Aggregate scores did not differ significantly between unpaired males and females and the paired starlings (Mann-Whitney $U=20.0$, $n_1=5$, $n_2=11$, $P=0.43$). No adults abandoned their nestbox after the trials.

Female and extra-bird involvement

Females aided in communal defense. Of the nineteen extra birds from other conspecific nests that responded to the experimental trials, eleven were males (three of which were banded), three were females (two that were banded), and five were of an unknown sex. The number of known females that responded to the trials was significantly different from zero (3/14; binomial test). The P value was <0.05 when doing a binomial test of females to total banded birds. In two separate cases, banded birds were confirmed to be nearby neighbours provisioning in their own nest box a few meters away.

Significantly more birds (other than parents) responded to the experimental than to the control trial (experimental range: 0-7 birds vs. control range: 0 birds). Similarly, extra birds were present more often during the experimental trials (56.3%) than the control (0%) trials (Fisher's Exact test $P = 0.0008$).

Aggregate scores and provisioning efforts

For the experimental trials, no correlation was found between the aggregate scores and the a) average total parental provisioning effort per nest (Pearson correlation $r = -0.087$, $n = 16$, $P = 0.75$) or b) average provisioning effort per nestling (Pearson Correlation $r = -0.033$, $n = 16$, $P = 0.90$). Similarly, no significant relationship for experimental trials was detected between aggregate scores and either the number fledged (Pearson correlation $r = -0.1503$, $n = 16$, $P = 0.58$) or the proportion fledged (Pearson correlation $r = -0.1126$, $n = 16$, $P = 0.68$). Parametric tests were used for aggregate scores as experimental trial scores were normally distributed.

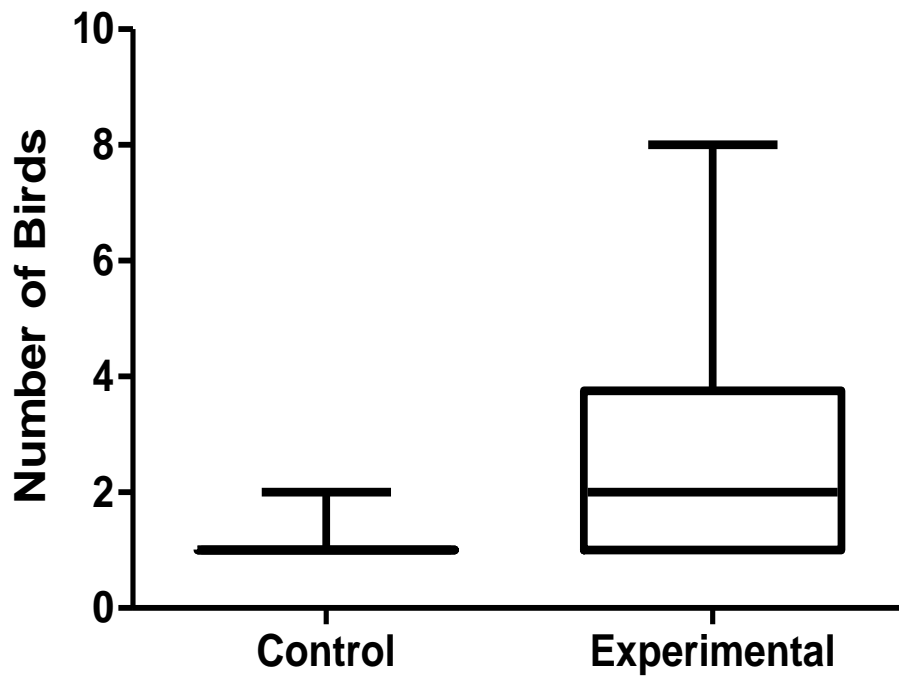


Figure 1. Total number of birds present during each of 16 control and experimental trials. Bar is max value and box plot is 25th and 75th percent quartiles.

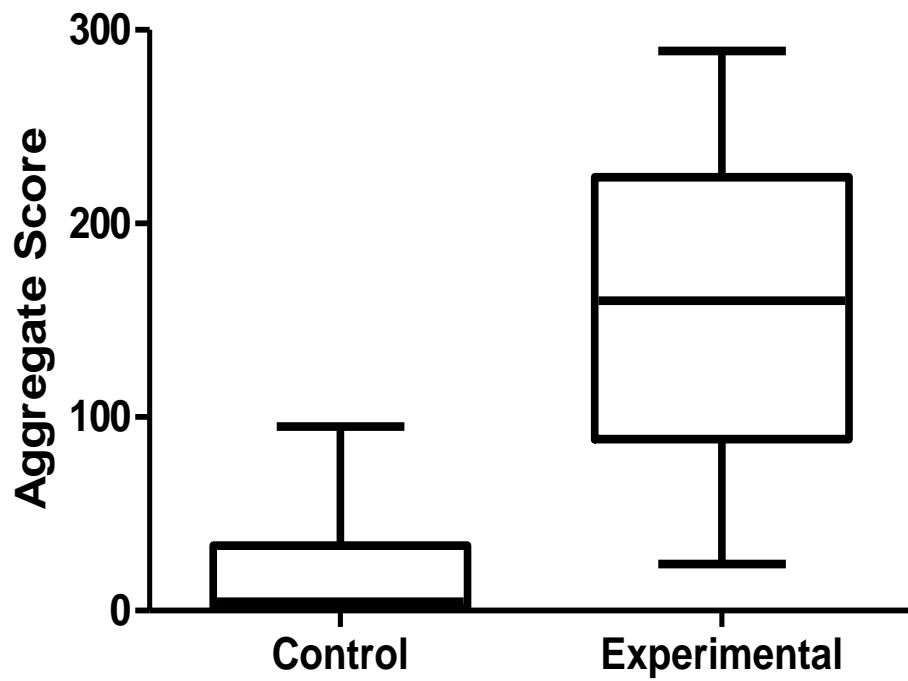


Figure 2. Aggregate scores from each of 16 control and experimental trials. Bar is max value and box plot is 25th and 75th percent quartiles.

DISCUSSION

Predator recognition by Starlings

Significantly more European starlings flew to the focal nestbox during the experimental than the control trials. Similarly, extra birds were present more often during the experimental trial. Also, significantly higher aggregate scores were found for the experimental than the control trials, all suggesting that the taxidermy Red squirrel was an effective predator model. Like this study, Siderius (1993) used a taxidermy crow to test nest defense in the Eastern kingbird (*Tyrannus tyrannus*). Neudorf & Sealy (1992) also used taxidermy mounts of various avian species for the experimental trial in order to test the threat of predation and parasitism. This research and research alike suggest that taxidermy mounts can be used effectively in experimental trials to elicit responses in passerine species. Similar studies (eg. Neudorf and Sealy, 1992) also use taxidermy mounts of objects that do not pose a threat for the control trial as well. Comparably for this study, the rock served as a functional control object as there was no defensive response from the Starlings.

There was a tendency for female social parents to respond more often to the Red squirrel model than male parents, although there was no significant difference between the two. This finding may coincides with the literature suggesting that females are often more heavily invested in the offspring than males (e.g. Clutton-Brock, 1991; Queller, 1997; Kokko & Jennions, 2012). Similar results were found in Red-winged blackbirds (*Agelaius phoeniceus*); females spent significantly more time close to the models, keeping a close watch than did males during the nestling stage (Neudorf & Sealy, 1992).

Paired vs. Unpaired

Surprisingly, the aggregate scores of paired adult starlings did not differ significantly during the experimental trials from those of unpaired adults. Though these results did not correspond with my initial prediction, the cooperative neighborhood hypothesis (Eliassen & Jorgensen, 2014) does predict that nearby neighbors would aid in nest defense. The starlings that did not have a social mate were documented to have help from other nearby neighbors three out of five times, which may have increased their aggregate scores, therefore altering the results from my initial prediction. However, this result may have not been too surprising given the range of extra birds as the unpaired nests could result with the same number of birds present during a trial as the paired nests.

Communal nest defense in Starlings

The results of this study suggest that communal nest defense occurs in European starlings; parents as well as other male and female conspecifics attacked the predator model. Females helped defend conspecific nests from the predatory threat, which supports one of the central predictions of the cooperative neighborhood hypothesis – that communal defense would occur when genetic offspring could be produced in conspecific nests. This study is novel in that it was able to test this prediction of the cooperative neighbourhood hypothesis not only with males, but also with females because female starlings produce genetic offspring in conspecific nests.

During the experimental trials, significantly more birds (other than parents) flew in to respond compared to control trials. There were up to seven extra birds

responding in one trial. Similarly, the number of times extra birds present during the experimental trial was significantly higher than for control trials. These findings support Eliassen & Jorgensen (2014) study and my hypothesis suggesting that birds other than the parents would be willing to help in defensive nest strategies outside of their social nest. This result may be due to the EPCs (Smith & Von Schantz, 2012), intraspecific (Pinxten et al., 1993 B; Sandell & Diemer, 1998; Yom-Tov et al., 1974), and quasi-brood parasitism (Griffith et al., 2004; Otter et al., 2011) that have been documented to take place within breeding passerine communities, including European starlings.

In two of the trials, the extra birds responding were confirmed (from band combinations) to be nearby neighbors who had their own brood in nestboxes. Defensive strategies such as mobbing and alarm calling are physically demanding on birds and may be dangerous or give away location (Curio, 1978). They also take the focus away from the care that could be provided to their primary nest. Therefore, it may be safe to assume that a bird may not take part in defensive behaviours unless there are benefits for them, such as protecting their genetic young in conspecific nests (Eliassen & Jorgensen, 2014), or perhaps aiding their relatives (Rohwer et al., 1976).

Many of the birds (both male and female) who aided with mobbing were banded and part of the starling community on campus. Similar studies on Red-winged blackbirds (Beletsky & Orians, 1989) and Great tits (*Parus major*) (Grabowska et al., 2012 a, b) found advantages to birds breeding with familiar neighbours. This included an increase in predator mobbing when birds bred with

other birds that they have encountered in previous breeding seasons. Many birds in this European starling community have been documented to return to the campus year after year to breed and fledge their young, giving reason to believe the starlings may recognize each other from previous seasons which may increase the amount of effort put into public good.

Eliassen & Jorgensen (2014) also predicted that EPP is strongly correlated with breeding density. The Saint Mary's campus has 39 nestboxes on trees. There are also several natural cavities that cannot be accessed with much ease and are therefore not included in this research. Some of these nestboxes are very close with natural cavities being in the same tree. This region of Halifax also provides many potential nesting sites for starlings that are not located on campus but nearby. I believe that the breeding density of the Saint Mary's campus is quite high due to the starling's ability to successfully fledge nestlings on the campus. Many households around the area will actively work to push breeding birds away from their property, as they may be a nuisance. However, as an active research site we enthusiastically work to encourage the Starlings to breed on campus. An increased breeding density would also permit increased likelihood of EPP in the community (Eliassen & Jorgensen, 2014), which in turn may increase communal nest defense.

Aggregate score comparisons

No relationship was detected in aggregate scores and overall parental provisioning effort per nest or per nestling. Similarly, no relationship was found between aggregate scores and either the number or proportion of nestlings fledged. I had predicted a positive relationship between these variables as higher aggregate

scores would indicate higher levels of parental investments and therefore would likely result in increased reproductive success. However, perhaps those birds with a lower aggregate score but high provisioning rates and/or reproductive success did not engage in as many EPCs, and therefore the number of extra birds responding to the predator threat was lower. The aggregate score depended on a variety of factors such as the number of alarm calls and chips might have been highly dependent on the number of birds present. Further research is needed in actual predator situations to determine if the number of birds defending the nest does impact the survival of the nestlings.

Conclusion

To conclude, adult European starlings responded defensively significantly more often to the predator model than to the rock. Female as well as male neighbors aided in communal nest defense, supporting one of the main predictions of the cooperative neighborhood hypothesis. Therefore, one direct benefit for engaging in different reproductive strategies may be that of enhanced communal nest defense, but other hypotheses would still need to be tested. Future research should include assessing the maternity and paternity of offspring to determine whether their genetic parents aided in their nest defense and if kin-selection of any kind was taking place by extra birds present in trials. It may also be beneficial to examine the reaction by Starlings when a predator is presented somewhere other than the nest box, such as a tree near by. Trials could include playing life-like noises, releasing scents or using other known predators to starling nestlings. Finally, comparing the mobbing response of European starlings to other types of passerines would be

beneficial in determining if female Starlings are the only bird to defy the predictions of the cooperative neighbourhood hypothesis.

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