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Nest defense, personality, and fitness of a locally endangered island passerine

Nicole M. Suckow[1,2] ⓘ | Henry S. Pollock[1,2] | Mark E. Hauber[1] | Martin Kastner[3] | Julie A. Savidge[4] | Kayla Baker[3] | Haldre S. Rogers[3]

[1]Department of Ecology, Evolution, and Behavior, School of Integrative Biology, University of Illinois at Urbana-Champaign, Champaign, Illinois, USA

[2]Department of Natural Resources and Environmental Sciences, University of Illinois at Urbana-Champaign, Champaign, Illinois, USA

[3]Department of Ecology, Evolution, and Organismal Biology, Iowa State University, Ames, Iowa, USA

[4]Department of Fish, Wildlife & Conservation Biology, Colorado State University, Fort Collins, Colorado, USA

Correspondence
Nicole M. Suckow, Department of Natural Resources and Environmental Sciences, University of Illinois at Urbana-Champaign, Champaign, IL, USA.
Email: nicolesuckow@gmail.com

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Abstract

Personality, or repeatable variation in behavior, may impact an animal's survival or reproduction. Parental aggression is one such personality trait with potentially direct implications for fitness, as it can improve offspring survival during vulnerable early life stages. We took advantage of a long-term nest box and fledgling survival monitoring project to explore the potential fitness consequences of both repeatability and variation in parental aggression in breeding pairs of a locally endangered passerine species (Såli: Micronesian starling, *Aplonis opaca*) in the presence of an invasive predator, the brown treesnake (*Boiga irregularis*), on the island of Guam. To do so, we tested for associations between aggressive offspring defense throughout the nesting cycle and three fitness measures: hatching success, fledging success, and post-fledging survival. Aggression varied greatly among breeding pairs and was repeatable within pairs ($R = .47$), providing evidence of a personality trait. Consistent with parental investment theory, nest stage was the best predictor of parental aggression, which increased with offspring age. Aggression was positively correlated with hatching success during the egg stage, but not nestling or post-fledging survival. We propose that parental aggression was decoupled from nestling and fledgling survival because parents were unable to defend young from nocturnal, invasive brown treesnakes. More broadly, our findings demonstrate that repeatable variation in personality traits may not necessarily confer fitness benefits, particularly in the presence of invasive predators.

KEYWORDS
brown treesnake, Micronesian starling, nest success, parental behavior, personality, post-fledging survival

1 | INTRODUCTION

Consistently repeatable patterns of individual behavior, also referred to as personality, can be adaptive or maladaptive depending on the social and environmental contexts (e.g., parental care, antipredator defense, mating, etc.) in which these behavioral traits are displayed (Sih et al., 2004). The impact of an individual's personality on their overall fitness can also be tied to environmental factors like resource availability; for example, when exploratory or aggressive behaviors provide a competitive advantage in terms of resource acquisition

(Dingemanse et al., 2004; Sih et al., 2004). Conversely, these same personality traits can be energetically costly and increase risk of injury or predation in other contexts (Burns et al., 2016; Robertson et al., 1986). Individual variation in behavioral phenotypes within a population may shift depending on fitness tradeoffs, and selective pressures acting on personality traits could have implications for population dynamics over time (Sih et al., 2004). Potential ecological and evolutionary consequences of variation in personality include altered demography, distributional range shifts, and the evolution of life-history traits (Wolf & Weissing, 2012).

Parental aggression in defense of vulnerable young is one key personality trait that can influence fitness. Aggressive behaviors such as physical attacks, mobbing, and alarm calls may reduce the chance of losing offspring to predation or nest parasitism (Avilés & Parejo, 2011; Lawson et al., 2020; Montgomerie & Weatherhead, 1988). Indeed, increased parental aggression has been associated with higher offspring survival rates among lizards (Sinn et al., 2008) and mammals (Watts et al., 2009) and higher reproductive success in birds (Betini & Norris, 2012; Kontiainen et al., 2009; Wiklund, 1990). Such evidence suggests that aggressive parents are often more effective at protecting their young, or alternatively, that aggression may be part of a behavioral syndrome related to better parental care, such as increased exploratory behavior or higher offspring provisioning rates (Hollander et al., 2008; Krieg & Getty, 2020). Parents may modulate their aggression based on how much they have invested in their young, with offspring age, brood size, or offspring quality as possible factors, or the risk of predation to their young (Kleindorfer et al., 2005; Montgomerie & Weatherhead, 1988; Shew et al., 2016). For example, parental investment theory predicts that larger, older offspring will be more valuable and should elicit greater defense from the parents (Montgomerie & Weatherhead, 1988). However, while many studies have found that parental aggression can benefit reproductive fitness, others have demonstrated that aggression can decrease reproductive fitness via tradeoffs with provisioning or clutch size (Thys et al., 2019; Wischhoff et al., 2018).

Understanding whether and how individual personality affects fitness may be relevant to wildlife conservation. For example, a study of a reintroduced bird population (of the New Zealand endemic hihi: stitchbird, *Notiomystis cincta*) on Tiritiri Matangi Island found that juveniles experimentally provided with supplementary carotenoids had both higher levels of boldness and higher subsequent probability of surviving to adulthood (Richardson et al., 2019). In some cases, anti-predator training may be an effective tool for helping native species recognize and respond adaptively to both native and novel predators (Blumstein et al., 2019; Greggor et al., 2021). Nevertheless, it remains poorly understood if and how variation in personality, and parental behavior in particular, can help conservation management of native populations threatened by invasive predators.

Here, we tested the hypothesis that parental aggression could impact the fitness of a locally endangered island passerine (Såli: Micronesian Starling, *Aplonis opaca*) by increasing offspring survival. The Pacific island of Guam experienced devastating losses to its native avifauna when the invasive brown treesnake (*Boiga irregularis*) was

introduced following World War II, resulting in the total extirpation of 10 of 12 native forest bird species (Savidge, 1987; Wiles et al., 2003). The Såli is one of two such species that has persisted and has been making a recovery on Guam due to its tolerance for urbanization coupled with localized snake control measures, in particular on Andersen Air Force Base in northern Guam (Pollock et al., 2021). Såli eggs and nestlings experience low predation rates due to adults choosing relatively safe nest site substrates in urbanized areas, such as predator-resistant nest boxes and streetlamp posts (Savidge et al., 2022). However, fledglings and young juveniles continue to suffer considerable mortality due to predation by brown treesnakes and feral cats (Pollock et al., 2019; Wagner et al., 2018). Nesting adult Såli on Guam exhibit variable levels of parental aggression towards diurnal intruders at the nest (including humans; H. S. Pollock & M. Kastner, personal observations), and in the current study, we asked whether parental aggression affected offspring fitness by way of hatching success, fledging success, and post-fledging survival. We hypothesized that parental aggression could impact offspring in two ways: (1) via a *direct* pathway like attacking predators and/or teaching offspring to evade predation or (2) via an *indirect* pathway such as a behavioral syndrome associated with improved parental care traits, like higher provisioning rates.

To explore the influence of parental aggression on offspring fitness in Såli, we first used repeatability analyses to test for consistent patterns of personality among breeding pairs. Second, to explore what life history factors predicted variation in aggressive behavior, we tested for associations between aggression and traits related to parental investment (offspring body mass, clutch size, and stage of the nest). We predicted a positive relationship between parental investment and aggression, with larger offspring, larger clutches, and clutches farther along in the nesting period associated with higher levels of aggression. Finally, to evaluate the possible fitness impacts of aggression, we tested for associations between parental aggression during the nesting period and (1) hatching success, (2) fledging success, and (3) post-fledging survival. If parental aggression is linked to offspring fitness via a *direct* pathway, we predicted that there would be a positive relationship between aggression and fledgling survival, since fledglings are free-living and more vulnerable to predation than eggs or nestlings in predator-resistant nest boxes. If parental aggression is linked to offspring fitness via an *indirect* pathway, we predicted that there would be a positive relationship between aggression and hatching/fledging success by means of a behavioral syndrome such as increased provisioning rates. As a corollary, we predicted that if more aggressive parents were better at provisioning offspring, then aggression would be positively correlated with offspring body condition.

2 | METHODS

2.1 | Study site and study species

We studied Såli, an omnivorous passerine in the starling family (Sturnidae), on Guam, the southernmost and largest island of the Mariana archipelago in the Western Pacific Ocean. Guam has a

tropical climate (mean annual temperature ± SD = 27.45 ± 0.52°C; USA National Weather Service, https://w2.weather.gov/climate/) with a wet season from July to December and dry season from January to June. Såli are cavity-nesters that breed year-round and exhibit biparental care (Jenkins, 1983). We observed and recorded parental aggression at Såli nest boxes (n = 62 boxes, 686 total nesting attempts) over the course of 4 years (April 2016–May 2020) on Andersen Air Force Base (hereafter, AAFB), an 8,100-ha military installation located in northern Guam (13.57°N, 144.92°E). Habitats on AAFB include urbanized areas, a golf course, and mixed secondary and primary limestone forest. The majority of Guam's Såli population (>90%; Pollock et al., 2021) nests and roosts on AAFB. Starting in 2015, nest boxes were installed on AAFB as part of a conservation project to increase Såli nest success (Savidge et al., 2022). Current major predators of birds on the island include non-native brown treesnakes and feral cats. Historically, native predators have included Hilitai (monitor lizards, *Varanus tsukamotoi*) and Åga (Mariana crows, *Corvus kubaryi*) (Dryden, 1965; Faegre et al., 2020; Weijola et al., 2020), both of which are exclusively diurnal.

To prevent predators from reaching the nest contents, each nest box was fastened to either a concrete utility pole (n = 50), which brown treesnakes could not climb, or an electric metallic tube (EMT) pole with a predator guard (n = 25), which greatly diminished, but did not completely prevent nest predation by brown treesnakes (8 likely predation events out of 686 total nesting attempts; J. A. Savidge and T. F. Seibert, unpublished data).

2.2 | Nest monitoring protocols

Nest boxes were monitored every 2 weeks and active nests were generally checked every 3–4 days. While repeated exposure to humans can potentially cause habituation, this population has already acclimated to inhabit an urban area. Moreover, the span of our study, specifically the large sample size and duration, minimizes the risk of our monitoring affecting results. During each nest check, we recorded the number of eggs and live young present. When live young were present, the nest stage was categorized by the status of nestling plumage development (Figure 1). Nestlings were categorized as new young (NY), partially feathered young (PY), or feathered young (FY) following Martin et al. (2013). Furthermore, at 15 days post-hatching, we banded each nestling, measured its right tarsus using digital calipers (model IP54, EAGems; accuracy ±0.01 mm), and weighed it using a digital scale (AWS-201, American Weigh Scales; accuracy ±0.01 g). We then calculated the scaled mass index (following Peig & Green, 2009) as an index of body condition to be used in the statistical analysis. Known information on the average incubation and nestling periods (~15 and 25 days, respectively; Savidge et al., 2022) was used to estimate when nestlings were expected to fledge. A clutch was deemed successful if one or more nestlings fledged (Dinsmore et al., 2002; Mayfield, 1975). Longitudinal monitoring over the course of the study has indicated breeding pairs have high nest site fidelity, and generally breed at the same box or use a pair of adjacent nest boxes.
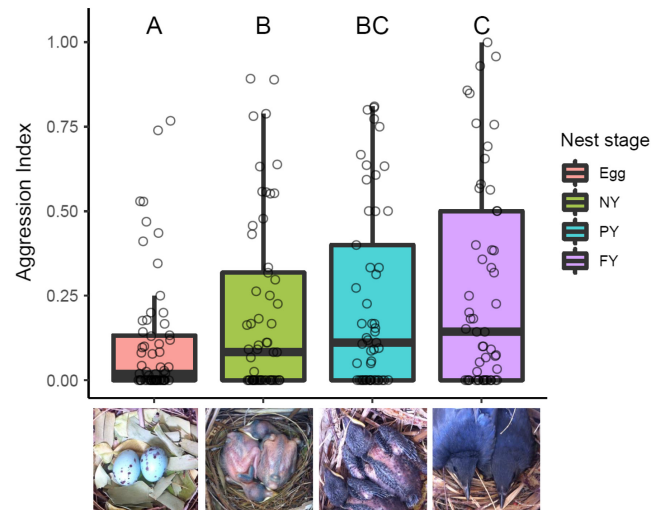
FIGURE 1 Aggression index by nest stage (egg, new young—NY, partially feathered young—PY, and feathered young—FY) for the 62 breeding pairs of Såli sampled at Andersen Air Force Base, Guam, USA from 2016 to 2020. Letters indicate significant post hoc differences (α = .05) among the four nest stages as determined by post-hoc tests on estimated marginal means

2.3 | Assessing parental aggression

For this study, we recorded parental aggression as a binary response based on the presence (1) or absence (0) of aggressive behaviors towards a human observer during each nest check. While animal personality research often uses the term "boldness" to describe responses to predators and "aggression" to describe responses to competitors or conspecifics (Réale et al., 2007), we use the term "aggression" in our description of Såli nest defense aimed at humans (potential predators). Much of the literature on nest defense differentiates aggressive from passive defense strategies. Several other studies observing intense, agonistic behavior similar to that of Såli in our study system, describe such nest defense behaviors aimed at potential predators as "aggressive" (Kazama et al., 2012; Knight et al., 1987; Kontiainen et al., 2009; Shew et al., 2016). We therefore used nest defense as an indicator of aggressive personality, and our use of "aggression" hereafter refers to the aggressive defense of vulnerable young by adult breeding pairs of Såli. The breeding pair was classified as aggressive if at least one Såli parent was present and exhibited agonistic behavior towards the observer. Observers were consistent within years, but varied somewhat between years. However, all observers were trained using the same protocol and assessed aggression based on the very distinctive agonistic behavior of Såli parents flying directly at (dive-bomb), or swooping by (fly-by) the observer, both of which were always accompanied by an alarm call, thus there was little room for ambiguity in interpretation of aggressive behavior. We studied personality of the breeding pair instead of individual personality because not all parent birds were banded and thus identifiable at the individual level. As a result, we also were unable to distinguish variation in aggressive behavior between males and females, as Såli are not discernibly sexually dimorphic. We

only documented nine cases of known turnover in banded breeding birds over the 4-year study period, or the equivalent of 2.25 turnover events per year. Most cases of observed turnover appeared to consist of a single individual replacing one member of the pair, so there was likely to be at least some continuity in aggressive behavior at those boxes. We are confident that these nine turnover events were the only ones occurring among banded birds, given that in all cases, re-nesting was delayed for at least several weeks following a turnover event compared to the typical re-nesting interval (Savidge et al., 2022). Furthermore, adult survival in our population is very high ($\bar{x}$ = 88%, n = 14 radio-tagged adults; H.S. Pollock, unpublished data), and most banded individuals continue to occupy the same nest boxes where they were banded in past years. Nevertheless, we acknowledge that there may have been additional turnover among unbanded pairs, and we were unable to account for this uncertainty in our study, so we did not account for turnover and considered breeding pairs as the statistical unit in our subsequent analyses.

2.4 | Monitoring post-fledging survival

To determine post-fledging survival, we used radio-telemetry to track one randomly selected nestling from each successful clutch. At 22–23 days post-hatching (2–3 days before fledging; Pollock et al., 2019), focal nestlings were fitted with a radio transmitter (1.8 g, BD-2, Holohil Systems) using a leg-loop harness (modified from Rappole & Tipton, 1991). The combined weight of the transmitter and harness was kept below 4% of fledgling body mass (3.25 ± 0.34%), following Barron et al. (2010). We monitored each radio-tagged fledgling every 1–2 days for the duration of the post-fledging period ($\bar{x}$ = 21.7 days; Pollock et al., 2019). Fledglings were located using a handheld telemetry receiver (model R-1000; Communications Specialists) and 3-element Yagi antenna (Wildlife Materials). Survival was confirmed by resighting, using color band combinations to verify the fledgling's identity. In the case of mortality, we recovered the radio-transmitter and documented the cause of death when possible.

2.5 | Statistical analyses

To determine whether breeding pairs of Såli exhibited consistent personalities with respect to nest aggression, we ran a repeatability analysis using the *rpt* function in the R package rptR (Stoffel et al., 2017). Repeatability, or intraclass correlation (ICC), is a metric calculated by partitioning within-group and between-group variances and is often used for estimating the maximum value of heritability of a trait (Bell et al., 2009). Here, we took a conservative approach and restricted the repeatability analysis to breeding pairs with $n \geq 10$ cumulative nesting attempts (n = 38 of 62; mean ± SD = 19.3 ± 5.94). We constructed a generalized linear mixed model with a binomial error structure (0 = not aggressive, 1 = aggressive) and pair ID as the grouping factor (random effect). Because we were measuring aggression across multiple years, across multiple nesting attempts

within a given year, and across multiple nest stages within a given nesting attempt, we included three fixed effects in our model to account for possible temporal dynamics of aggression. First, we included sampling year (2016, 2017, 2018, 2019, and 2020) in case aggression varied systematically across years. Second, we included the ordinal number of nesting attempts within a given year as a continuous variable to account for possible shifts in aggression related to cumulative reproductive investment. Finally, we included nest stage (egg, NY, PY, and FY) to account for possible increases in aggression with increasing parental investment in a given clutch. We ran the model for n = 1000 bootstrap samples to estimate uncertainty in repeatability of aggression and generate 95% confidence intervals.

To assess predictors of variation in aggressive behavior among breeding pairs of Såli, we generated a stage-specific "aggression index" (hereafter AI, calculated as the proportion of all nest checks at a given nest stage in which the pair exhibited aggression) for each breeding pair at each of the four nest stages. We then ran a generalized linear mixed model using the *glmmTMB* function in the R package glmmTMB (Brooks et al., 2017). Because AI was a proportion bounded by 0 and 1, we ran a beta regression model with a logit link function. The model included stage-specific AI (i.e., for a given nest attempt, there were four AI measurements—egg, NY, PY, and FY) as the response variable, average scaled mass index of nestlings (Peig & Green, 2009), stage-specific clutch size (the number of viable eggs or nestlings present at a particular stage of a nesting attempt), and nest stage as fixed effects, and pair ID as a random effect (Table S1). We used Wald Chi-Squared tests with α = .05 to assess significance of each of the three fixed effects and Tukey's post-hoc tests to assess differences in aggression across the four nest stages.

We tested for the predicted positive relationship between stage-specific AI and three fitness-related metrics: hatching success, fledging success, and post-fledging survival. All three metrics were derived from the same sample of offspring. We split the traditional measure of nesting success into hatching and fledging success because we found that virtually all failure at the egg stage was due to chronic hatching failure among select breeding pairs, which exhibited low levels of aggression. To control for the potential influence of chronic egg failure on parental aggression during the incubation phase, we compared a hatching success model that included all breeding pairs (n = 38) to a model with chronic nest failures removed (n = 27) and found no statistically significant differences (p > .05), so we retained the full dataset of 38 breeding pairs for our analysis. We calculated daily survival rates (DSR) for the egg stage (~15 days) and the nestling stage (~25 days), for each breeding pair using the program MARK (White & Burnham, 1999) implemented in the package RMark (Laake, 2013). For each metric, we compared three temporal models of DSR: constant DSR, linear trend in DSR, and a quadratic trend in DSR. We found that the constant DSR model was the best supported in both cases, and so we report results from constant DSR models for each fitness metric. We then calculated hatching success for each breeding pair by exponentiating egg stage DSR estimates for each breeding pair over the 15-day incubation period (nest success = DSR^{15}) and

fledging success by exponentiating nestling stage DSR estimates over the 25-day nestling period (nest success = DSR^{25}). To test for relationships between aggression and hatching/fledging success, we ran two beta regression models: one that included hatching success as the response variable and egg-stage AI as the fixed effect, and a second that included that included fledging success as the response variable and nestling-stage AI as the fixed effect. With respect to post-fledging survival, sample sizes were too small (range: 1–8; mean $\pm$ SD = 3.7 $\pm$ 1.6) to model using survival analysis, so instead, we calculated raw post-fledging survival rates. These survival rates were determined by dividing the number of fledglings that survived the post-fledging period by the total number of fledglings radio-tagged per monitored pair. To test for a relationship between AI and the proportion of fledglings that survived the post-fledging period, we ran a beta regression model that included raw post-fledging survival as the response variable and fledgling-stage AI as the fixed effect. We used Wald Chi-Squared tests with $\alpha = .05$ to assess significance for all models.

2.6 | Ethics statement

All research was approved by the Institutional Animal Care and Use Committee (IACUC) at Colorado State University (IACUC #17-7176A).

3 | RESULTS

3.1 | Variation and repeatability in aggression among breeding pairs

We found substantial variation in aggression rates across the 62 breeding pairs of Såli (Figure S1). The aggregate AI ranged from 0 (never aggressive) to 0.84 (consistently and highly aggressive) across the population (mean $\pm$ SD = 0.16 $\pm$ 0.22; Figure S1). After controlling for sampling year, nest stage, and ordinal nesting attempt, we found that aggression was repeatable among the 38 breeding pairs with $n \geq 10$ nesting attempts ($R = .47$; 95% CI = 0.28–0.56).

3.2 | Predictors of variation in parental aggression

Nest stage was a significant predictor of variation in parental aggression ($df = 4$, $\chi^2 = 36.4$, $p < .0001$), with aggression increasing throughout the nesting period (Figure 1; Figure S2). Tukey's post-hoc tests revealed that AI was significantly lower at the egg stage relative to all other stages with the highest AI recorded at the FY stage (Table 1). In contrast, neither nestling body condition, as measured by the scaled mass index ($df = 1$, $\chi^2 = 0.06$, $p = .80$) nor mean clutch size was predictive of variation in parental aggression ($df = 1$, $\chi^2 = 0.22$, $p = .64$).

TABLE 1 Mixed model output from beta regression (including breeding pair ID as a random effect) testing for pairwise differences in aggression among the four nest stages (egg, new young—NY, partially feathered young—PY, and feathered young—FY)

| Comparison	β ± SE	z	p
Egg-NY	**0.59 ± 0.19**	**3.2**	**.007**
Egg-PY	**0.78 ± 0.19**	**4.0**	**<.001**
Egg-FY	**1.14 ± 0.19**	**5.9**	**<.001**
NY-PY	−0.19 ± 0.18	1.1	.70
NY-FY	**0.55 ± 0.19**	**3.1**	**.01**
PY-FY	0.35 ± 0.17	2.0	.17

Note: The beta estimates, *z* value and *p* value are listed for each comparison. Significant differences as determined by Tukey's post-hoc tests are indicated in bold.

3.3 | Correlations between parental aggression and fitness

Among our three fitness metrics, fledging success was highest (mean $\pm$ SD = 0.92 $\pm$ 0.09), hatching success was intermediate (mean $\pm$ SD = 0.75 $\pm$ 0.22), and post-fledging survival was lowest (mean $\pm$ SD = 0.23 $\pm$ 0.23). We found a significant positive correlation between egg-stage AI and hatching success ($df = 1$, $\chi^2 = 13.9$, $p = .0002$; Figure 2a), with more aggressive pairs having higher hatching success. However, parental aggression was not correlated with fledging success ($df = 1$, $\chi^2 = 0.03$, $p = .86$; Figure 2b) or post-fledging survival ($df = 1$, $\chi^2 = 0.02$, $p = .90$; Figure 2c).

4 | DISCUSSION

Breeding pairs of Såli on Guam exhibited variable and repeatable patterns of aggressive behaviors when defending their nest sites, providing strong evidence of a personality trait. Nest stage was an important predictor of parental aggression, with older offspring eliciting more aggression. In turn, we found that parental aggression was positively correlated with hatching success, but not with fledging success or post-fledging survival. The lack of relationship between post-fledging survival and nest aggression suggests that *direct* fitness benefits of parental aggression are unlikely; that is, parents probably cannot fend off brown treesnakes or cats. Since we documented no known egg predation events at nest boxes, the positive correlation between aggression and hatching success is likely *indirect*, possibly via a behavioral syndrome of other traits associated with enhanced parental care. Because offspring were often depredated soon after fledging (Pollock et al., 2019), when parental aggression was highest, carry-over effects of heightened aggression from the recently fledged brood may be driving the correlation between hatching success and parental aggression of the following clutch, although this hypothesis remains untested. Parental aggression was largely decoupled from post-fledging survival because parents are unable to defend vulnerable fledglings
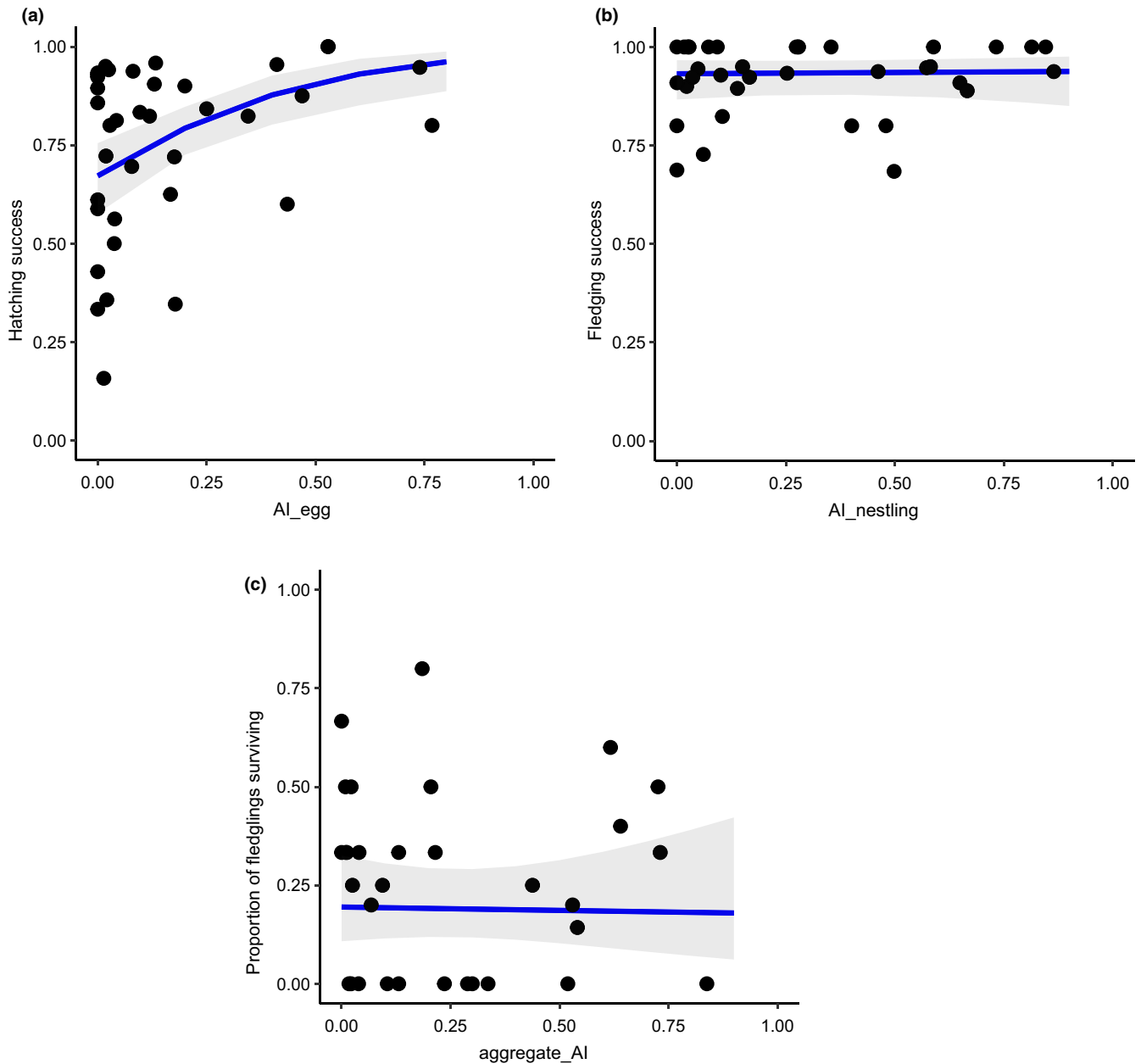
FIGURE 2 Relationships between (a) hatching success and egg stage aggression (AI_egg), (b) fledging success and nestling stage aggression (AI_nestling), and (c) post-fledging survival and aggregate aggression (aggregate AI) for the 38 breeding pairs of Såli with $n \geq 10$ nesting attempts sampled at Andersen Air Force Base, Guam, USA from 2016 to 2020. Lines of best fit are indicated in blue ±95% CI (shaded gray)

from nocturnal, invasive predators such as brown treesnakes and feral cats once they have fledged the predator-resistant nest boxes. Our findings suggest that repeatable variation in parental personality traits such as aggression may not necessarily provide direct fitness benefits to offspring or that the adaptive value of these traits may be diminished in the presence of evolutionarily novel predators.

Parental aggression was repeatable ($R = .47$) and varied widely among breeding pairs (aggregate AI range = 0–0.84), with some pairs exhibiting no aggression and others being consistently aggressive. The repeatability was higher than average in comparison to a meta-analysis of repeatability on behavioral traits across taxa ($\bar{x} = 0.37$; Bell et al., 2009). Såli pairs maintaining clear personalities throughout the study further suggests that our nest monitoring did not contribute to any problematic habituation. Similar avian nest defense studies have found aggression to be repeatable in species from multiple different orders (Clermont et al., 2019; Kazama et al., 2012; Kontiainen et al., 2009). Among breeding pairs of Såli, aggression differed predictably between nest stages as well, with parents behaving more aggressively at later stage nests, consistent with parental investment theory (Trivers, 1972). As the likelihood of offspring survival to independence increases, they become more

valuable to the parents, thereby eliciting greater offspring defense (Andersson et al., 1980). Conversely, clutch size did not serve as a predictor of parental aggression, likely due to little variation in clutch size: most clutches laid (~90%) contained two or three eggs (Savidge et al., 2022). Thus, Såli may instead be investing more in the quality of offspring over quantity for each clutch, as is typical in tropical birds (Jetz et al., 2008).

We found evidence that variation in parental aggression was positively related to hatching success at the egg stage. More aggressive breeding pairs had higher hatching success, although the mechanism remains unclear. Because predator-resistant nest boxes kept eggs safe from predators, a direct benefit of increased aggressive behavior is unlikely. Instead, we posit that parental aggression could be part of a behavioral syndrome (*sensu* Sih et al., 2004) indirectly linking aggression to hatching success via increased nest attentiveness or improved nest incubation. Greater aggression has been tied to other beneficial behaviors such as increased exploration or higher provisioning rates (Cain & Ketterson, 2013; Hollander et al., 2008; Krieg & Getty, 2020; Wetzel & Westneat, 2014), which subsequently can improve offspring survival. However, parental aggression here was not associated with nestling body condition, as measured by scaled mass index, consistent with the lack of correlation between aggression and fledging success and suggesting that variation in aggression at the nestling stage is unlikely to confer fitness benefits through a behavioral syndrome such as increased provisioning rates. Because Såli have very rapid re-nesting rates, an alternative hypothesis for the correlation between aggression and hatching success is that pairs that have successfully fledged chicks have higher levels of aggression that carries over into the following nesting cycle. Future studies of the Såli population on Guam that quantify variation in other behaviors, namely incubation behavior, will be important for fully understanding the mechanistic link between parental aggression and hatching success.

In contrast to hatching success, neither fledging success nor post-fledging survival was correlated with parental aggression. Across our study population, parents increased aggression with offspring age and were more aggressive at the nestling versus egg stage. However, parental aggression was probably decoupled from fledging success due to the relative safety of the predator-resistant nest boxes, as >85% of offspring mortality occurred during the egg stage and most offspring that hatched ended up fledging successfully. Even if nests were unprotected, it is unlikely that diurnal parental aggression would have benefited nestling survival, because the most significant predators, brown treesnakes and feral cats, are nocturnal. During the post-fledging period, parental aggression was not correlated with survival of radio-tagged chicks, indicating that parental defense against predators does not appear to provide a direct benefit to fledglings.

Prior to the introduction of invasive vertebrate predators, nocturnal predation events were likely uncommon on Guam. Therefore, diurnal nest defense should have been a beneficial behavior for reducing predation of Såli eggs and nestlings by Guam's native predators, such as Hilitai and Åga (Dryden, 1965; Faegre et al., 2020;

Weijola et al., 2020). The introduction of novel nocturnal predators that hunt when adult Såli are roosting and less able to defend offspring is a selective pressure that effectively circumvents diurnal defense mechanisms. Furthermore, outside of the protected nest box, Såli fledglings, which are highly sedentary and relatively poor fliers, are vulnerable and essentially unprotected at night (Pollock et al., 2019). These findings indicate that invasive predators can partially dampen or counteract the adaptive benefits of personality traits such as aggression, which can have important conservation implications for threatened or endangered prey populations.

Finally, the documented relationship between aggression and hatching success in Såli on Guam begs the question of whether or not aggression is a heritable trait. Addressing this question is feasible in this system because Såli exhibit very high philopatry on AAFB, adults show high nest site fidelity, and all offspring from nest boxes are currently banded as part of a long-term monitoring project (M. Kastner, personal observations). To that end, longitudinal studies of aggressive behavior across generations, cross-fostering experiments with aggressive and non-aggressive pairs, or quantifying other metrics of parental care at the nest, including incubation and provisioning rates, could help gain a more comprehensive understanding of the factors that generate and maintain variation in aggressive behavior among Såli on Guam.

DATA AVAILABILITY STATEMENT

Data from this paper are available on the GitHub repository at the following URL: https://github.com/henRyPollock/Sali-parental-aggression.

ORCID

Nicole M. Suckow https://orcid.org/0000-0003-2395-1127

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