Does fluctuating selection maintain variation in nest defense behavior in Arctic peregrine falcons (*Falco peregrinus tundrius*)?

by

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Abstract

Within populations, individuals often exhibit repeatable among-individual differences in behavior, and in some cases, these are linked to different fitness outcomes. Several mechanisms have been proposed to contribute to the maintenance of repeatable among-individual variation in behavior. Here we study nest defense behavior in Arctic peregrine falcons (*Falco peregrinus tundrius*) over two successive breeding seasons (2018 and 2019) to evaluate the importance of three mechanisms that could underlie the maintenance of among-individual variation in this trait; state-dependence, assortative mating and fluctuating selection. Nest defense was measured as the response made by peregrines towards human observers during standard nest visits; high nest defense was characterized by close approaches to the observer, and low nest defense was characterized by maintaining greater distance from the observer. Nest defense scores ranged from 0m (i.e., contact with observer) to 600m. We found that nest defense was repeatable both within- (r = 0.37 and across-years (r = 0.19). Consistent with parental investment theory, both sexes exhibited state-dependent increases in their nest defense behavior with increasing nesting stage. Patterns of assortative mating and reproductive success varied greatly between the two study years. In the first year of the study (2018), peregrines mated assortatively; females with high levels of nest defense tended to pair with males that also had high levels of nest defense. However, the pattern reversed in 2019, and peregrines mated disassortatively. Additionally, we found that the fitness outcomes of nest defense differed between years. In 2018, peregrines with higher nest defense scores had a lower probability of fledging a nestling, and the opposite was true for 2019. Taken together, our results are consistent with fluctuating selection acting to maintain variation in nest defense behavior in peregrine falcons. We suggest that the fluctuating selection may result from an underlying trade-off between nest defense and other forms of parental investment, such as provisioning, with the overall benefit of nest defense (or provisioning) depending on year-specific environmental conditions. Although this study was only conducted over two years, they did differ markedly. The first year of the study (2018) had considerably fewer heavy rain events (N = 1), that can cause nestling mortality in this population, compared to 2019 (N = 11 heavy rain events). Consequently, there was lower overall reproductive success in 2019 compared to 2018. Future work is needed to assess the mechanism underlying fluctuating selection on nest defense in peregrine falcons.

Preface

This thesis is an original work by Nickolas A. Gulotta. No part of this thesis has been previously published. The data collected part of the thesis research received animal care approval from the University of Alberta Animal Care Committee under permit number AUP00000042.

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Chapter 1

Does fluctuating selection maintain variation in nest defense behavior in Arctic peregrine falcons (*Falco peregrinus tundrius*)?

1.1 Introduction

Within populations, individuals often exhibit consistent among-individual differences in behavior (i.e., animal personality) (Dall et al., 2004). Animal personality has been documented in taxa including fish (Francis, 1990; Wilson et al., 1993; Brown et al., 2005), mammals (Gosling, 1998; Weiss et al., 2000; Dochtermann and Jenkins, 2007) , and birds (Verbeek et al., 1994; Dingemanse et al., 2002; Drent et al., 2003) and for a range of behaviors, including nest defense (Kontiainen et al., 2009; Burtka and Grindstaff, 2013; Møller and Nielsen, 2014) and provisioning (Schwagmeyer and Mock, 2003; Nakagawa et al., 2007; Westneat et al., 2011). Consistent among-individual differences in traits such as nest defense can have important fitness consequences (Dingemanse et al., 2004; Both et al., 2005; Kontiainen et al., 2009). For example, in Ural owls (*Strix uralensis*), individuals that are more aggressive in nest defense have higher reproductive success than those that are less aggressive (Kontiainen et al., 2009). Several studies examining nest defense have revealed that individuals differ consistently in how they invest in this form of parental care (Dingemanse et al., 2004; Both et al., 2005; Kontiainen et al., 2009; Burtka and Grindstaff, 2013; Møller and Nielsen, 2014; Burtka and Grindstaff, 2015; Arroyo et al., 2017; Crisologo et al., 2017; Clermont et al., 2019a; Clermont et al., 2019b; Szasz et al., 2019). Given that predation of eggs and nestlings is a main contributor to nest failure in many bird species

(Montgomerie and Weatherhead, 1988), how can we understand the maintenance of consistent among-individual differences in nest defense? Four major (non-exclusive) classes of explanation have been proposed: trade-offs (Stearns, 1989), state-dependent behavior (Dingemanse and Wolf, 2010; Wolf and Weissing, 2010), assortative mating (Schuett et al., 2010), and fluctuating selection (Dingemanse et al., 2004). In this study, we assess support for the latter three (state-dependent behavior, assortative mating, and fluctuating selection) in maintaining consistent among-individual differences in nest defense in Arctic breeding peregrine falcons (*Falco peregrinus tundrius*).

Many adaptive explanations for consistent among-individual differences in behavior, including nest defense, are based on state-dependent behavior. Individual differences in states, including, age, nest site, energy reserves, and brood value, will lead to individual differences in the expression of behaviors whose payoffs vary with these measures of state (Dingemanse and Wolf, 2010; Wolf and Weissing, 2010). Differences in state that are stable (i.e., not easily changed or not able to be changed) such as sex, offer a simple explanation for among-individual differences since the state variable underlying the variation is consistent through time (Dingemanse and Wolf, 2010; Wolf and Weissing, 2010). For example, in Western bluebirds (*Sialia Mexicana)*, sex was a predictor of investment in nest defense across different breeding contexts (e.g., nest stage); males were more defensive on average than females (Duckworth, 2006). However, unlike sex, many other state variables are labile and individuals can express or experience different states at different times in their life. Brood value, can predict nest defense within a nesting season (Curio, 1987; Montgomerie and Weatherhead, 1988; Redondo and Carranza, 1989; Wiklund, 1990b; Rytkonen, 2002). For example, in Imperial shags (*Phalacrocorax atriceps)*, males were more aggressive in nest defense with increasing number and age of offspring (Svagelj et al., 2012). This pattern of increasing nest defense as a function of brood value is consistent with parental investment theory which predicts that increasing brood value should favor more investment into nest defense (Trivers, 1972; Montgomerie and Weatherhead, 1988). Brood value can also change due to natural variation in brood size (e.g., through nestling mortality), and birds can also adjust their investment in nest defense in response to this variation. For example, in Merlins (*Falco columbarius)*, experimentally enlarged broods were defended more intensely compared with experimentally reduced broods (Wiklund, 1990b). Many birds show year-specific variation in lay date (Nussey et al., 2005), and in Ural owls, females that laid eggs earlier in the season had larger clutches that were defended more intensely and subsequently had more nestlings fledge (Kontiainen et al., 2009). Despite the fact labile states are able to change, temporal consistency in labile traits is still possible (Dingemanse and Wolf, 2010; Wolf and Weissing, 2010). For example, an individual's initial state may give rise to differences in behavior that maintain or intensify initial state differences through a positive feedback (Dingemanse and Wolf, 2010; Wolf and Weissing, 2010; Sih et al., 2015). Indeed, some of the labile state characters that influence nest defense can vary consistently among individuals (e.g., lay date (Perrins, 1970; Nussey et al., 2005), clutch size (Lack, 1947, 1954; Ricklefs, 1968)).

Among-individual differences in nest defense could also be maintained through assortative mating, whereby the fitness of particular combinations of parent behavioral types (i.e., individuals mean phenotypic value for a behavioral trait) have higher success. Assortative mating was observed in Eastern bluebirds (*Sialia sialis*), who were more likely to pair with mates that had similar nest defense strategies and had higher reproductive success due to the pairing (Burtka and Grindstaff, 2015). Individuals of both sexes can share a preferred behavioral type if it indicates parental quality or improves offspring fitness (Schuett et al., 2010). Mating based on behavioral type can contribute to the maintenance of among-individual differences if both extremes of the phenotype (i.e., high aggression-high aggression, low aggression-low aggression) have similar fitness outcomes when paired (Schuett et al., 2010). This pattern of assortative mating was observed in Great tits (*Parus major*), whereby pairs of extreme behavioral types (i.e., high exploration-high exploration, low exploration-low exploration) had higher reproductive success than dissimilar behavioral types (Both et al., 2005).

In contrast, among-individual variation in nest defense could also persist through disassortative mating, whereby individuals prefer a mate that has a dissimilar behavioral type (Schuett et al., 2010). Disassortative mating can be adaptive if pairs are genetically or behaviorally incompatible, and females choose to pair with mates with dissimilar behavioral types to achieve an intermediate behavioral type for offspring while simultaneously achieving higher compatibility with their mate (Dingemanse et al., 2004; Both et al., 2005; Van Oers et al., 2008; Schuett et al., 2010). For instance, in captive breeding Cockatiels (*Nymphicus hollandicus*) that had free mate choice, pairs that mated disassortatively based on "agreeableness" (i.e., an aggregate measure of the tendency to be aggressive vs docile, submissive, and tolerant) had higher compatibility with their mate that resulted in increased reproductive success compared to pairs that had similar behavioral types (Fox and Millam, 2014). Although much of the support for mate choice maintaining among-individual variation is through assortative mating whereby similar behavioral types achieve higher reproductive success (Both et al., 2005; Schuett et al., 2011; Gabriel and Black, 2012; Kralj-Fišer et al., 2013; Burtka and Grindstaff, 2015), evidence exists that disassortative mating can be adaptive. However, disassortative mating will erode among-individual variation over time if the behavioral variation has genetic underpinnings (Schuett et al., 2010; Fox and Millam, 2014; Martin-Wintle et al., 2017), and thus can only explain the evolutionary maintenance of behavioral variation that arises via environmental effects.

Finally, different behavioral types could be maintained in populations under fluctuating selection such that alternative behavioral types achieve equal fitness on average (Dingemanse et al., 2004; Boon et al., 2007; Wolf and Weissing, 2010; Bergeron et al., 2013; Montiglio et al., 2014; Le Cœur et al., 2015; Nicolaus et al., 2016). Studies have found food availability (Dingemanse et al., 2004; Boon et al., 2007; Bergeron et al., 2013; Montiglio et al., 2014; Le Cœur et al., 2015) and population density (Nicolaus et al., 2016) can each act as key factors underlying fluctuating selection. For example, Dingemanse et al. (2004) found the maintenance of behavioral variation was attributed to fluctuating food availability, with fast exploring males having lower fitness in years with peak masting and higher fitness in years with lower food availability. Similarly, Nicolaus et al. (2016) found that fluctuations in Great tit population density acted to maintain among-individual differences, with slow explorers doing better in years with high densities and vice versa for years with low densities. Fluctuating selection is an intuitive explanation for the maintenance of behavioral types since many taxa experience temporal variations in their environment that directly impact food availability or population density thus allowing multiple optimal behavioral types to exist that are adapted for each ecological context while achieving equal fitness on average.

Here, we study nest defense in Arctic peregrine falcons (*Falco peregrinus tundrius*) in Rankin Inlet, Nunavut, Canada. First, we assess the short (within-year) and long-term (across-year) repeatability of nest defense. We evaluate support for state-dependence of nest defense by quantifying the relative importance of stable (i.e., sex) and labile (i.e., nest stage) states on the expression of nest defense behavior. Next, we used multivariate models to evaluate support for assortative mating. Under state-dependent adjustment of nest defense, we would predict within-individual changes in nest defense to positively covary since both parents at a given nest experience simultaneous shifts in labile state variables such as brood value, clutch size, and nest stage. We assessed support for the presence of assortative mating by estimating the among-pair correlation in nest defense behaviors. Under assortative mating, we predict a positive among pair covariance in nest defense, while under disassortative mating, we predict a negative among pair covariance in nest defense. Finally, we evaluated if nest defense predicted measures of reproductive success (i.e., probability of hatching at least one nestling, probability of fledging at least one nestling, number fledged, and nestling mass at fledging). We discuss our results in light of how they contribute to our understanding of the role of state-dependence, assortative mating, and fluctuating selection in maintaining variation in nest defense behavior in peregrine falcons.

1.2 Material and Methods

1.2.1 Study Species

Arctic peregrine falcons are long-distance migrants that winter in the southern United States, Mexico, and Central and South America, and breed throughout the North American Arctic, including Greenland (White, 1968; White et al., 2013). Peregrines arrive at our study site in Rankin Inlet, Nunavut, in mid-May and egg laying occurs during the first two weeks of June (Court et al 1988). Peregrines do not build nests. Though they will occasionally re-use Common raven (*Corvus corax*) and Rough-legged hawk (*Bueto lagopus*) stick nests, most peregrines in our study area nest in scrapes directly on the substrate. Arctic peregrines generally lay between 3 and 4 eggs (Court et al., 1988). The incubation period lasts approximately 36 days from when the first egg is laid (33 days from the fourth) (Jaffré et al., 2015), and hatching occurs asynchronously in the first two weeks of July (Court et al., 1988). Peregrines are long-lived and exhibit bi-parental care (Court et al., 1988; Franke et al., 2010). During the breeding season, raptors are central place foragers, and at least one adult is constrained to nest for incubation, brooding, feeding, and defense of eggs and altricial young (Enderson, 1973; Sonerud, 1992; Palmer et al., 2001; Slagsvold and Sonerud, 2007; Sonerud et al., 2014a; Sonerud et al., 2014b). In peregrine falcons, these behaviors are generally performed by females, and males are commonly engaged in foraging, in part due to pair-bonding, but also due to a short lethargic phase that is typically seen in females just before, and during egg-laying (White et al., 2002; Ratcliffe, 2010; Lamarre et al., 2017). Male peregrine falcons generally provision the female during incubation and early brood rearing (White et al., 2002). Further, female peregrines are approximately a third larger than males (Andersson and Åke, 1981; White et al., 2002), and are formidable defenders of eggs and young against typical intruders, such as Arctic foxes (*Vulpes lagopus*), Wolverines (*Gulo*

gulo), and Short-tailed weasels (*Mustela erminea*) in our study population.

1.2.2 Study Site

This study was conducted in a 455 km² area near the community of Rankin Inlet, Nunavut, Canada (62°49′N, 92°05′W), and is situated on the west coast of Hudson Bay. Part of the study area is encompassed within Hudson Bay which is dominated by a rugged coastline that provides suitable habitat for cliff-nesting species such as peregrine falcons, Rough-legged hawks, Canada goose (*Branta canadensis*), Common eider (*Somateria mollissima*), and Common ravens. Most of the study area is characterized by rolling upland hills and eskers that contain rugged rocky outcrops that are suitable for nesting (Court et al., 1988). The proximity to the coast and numerous lakes supports large numbers of Arctic ground squirrels (*Urocitellus parryii*), waterfowl, and seabird colonies.

Arctic peregrine falcon breeding in Rankin Inlet, Nunavut, Canada have been studied since the 1980s to understand their ecology and ecotoxicology following the widespread decline of peregrines from DDT (Court et al., 1988; Franke et al., 2010, 2011, 2013, 2016; Anctil and Franke, 2013; L'Herault et al., 2013; Anctil et al., 2014; Jaffré et al., 2015; Lamarre et al., 2017). Rankin Inlet has one of the highest breeding densities of peregrine falcons in the world with ~30 breeding pairs (one pair/15km²), believed to be due to the high availability of suitable nesting sites (Court et al., 1988; Franke et al., 2010). This population consumes both mammalian (e.g., Red-backed vole (*Myodes rutilus*), Northern collared lemming (*Dicrostonyx groenlandicus*), North American brown lemming (*Lemmus trimucronatus*), and Arctic ground squirrels) and avian prey (e.g., insectivorous birds, waterfowl, seabirds) (Bradley and Oliphant, 1991; Franke et al., 2010).

1.2.3 Fieldwork

Fieldwork began in mid-May for both 2018 and 2019 seasons and corresponded with the arrival of peregrines to Rankin Inlet from their annual migration from their southerly wintering grounds. A census of the known nesting sites was conducted at least twice per field season. Sites were considered occupied if one or more adults displayed territorial or reproductive behavior (e.g., vocalization and/or flight behavior associated with defense of breeding territory or presence of nest building, nest, or eggs) (following Franke et al., 2010). All unoccupied sites were checked until occupancy was confirmed or the breeding season was sufficiently advanced to conclude that the site was vacant (Franke et al., 2010). Once eggs were detected, we deployed RECONYX motion-activated cameras (Recoynyx, Holmen, WI, USA) at the nesting site (i.e., 2018: n = 28, 2019: n = 34). Occupied nests were visited every ~10 days to replace batteries and memory cards for the duration of the breeding season or until the nest had failed. Motion-activated cameras were used to document prey deliveries, clutch sizes, hatch dates, nest failures, and to read color bands on adults. Once nestlings hatched, a non-toxic colored mark was applied to one leg to track growth until fledging (Court et al., 1988; Anctil et al., 2014). Nestlings were banded at ~20 days old and were fitted with a U.S. Fish and Wildlife band (Court et al., 1988; Franke et al., 2010). We did not visit nests after ~25 days to avoid inducing early fledging.

1.2.4 Nest defense tests

Nest defense was assessed as part of regular nest monitoring (i.e., camera deployment and maintenance, and banding), and occurred during egg laying, incubation, and provisioning stages of the nesting cycle. For each visit, we recorded nest site ID, date, observer, travel mode (i.e., snowmobile, quad, or boat), nest approach direction (from above or below), and time. We did not assess nest defense when traveling by helicopter to remote nest sites since the disturbance could impact nest defense behavior. Next, we recorded the distance at which the nest became visible to observers. If a peregrine flushed from the nest during the approach, we noted the distance at which this occurred (i.e., flight initiation distance, or FID) to assess nest defence. FID is widely used in songbirds and raptors (Cavalli et al., 2016; Nordell et al., 2017). When observers arrived at the nest, they completed a 2-minute focal observation and recorded the number of times a focal bird stooped and the minimum distance at which the focal bird approached the observer (if the bird hit an observer, we recorded 0m). When conducting nest defense tests, two observers were present at the nest, one to monitor each parent. Assignment of observers to parents was done arbitrarily for each test. After the focal observation, birds were assigned a nest defense score on a 0-5 scale: 0— bird is absent, 1— bird is present but not vocalizing, 2— bird is vocalizing but not in flight, 3— bird is circling overhead with or without vocalizations, 4— stooping toward observer, 5—hitting or near miss of the observer. Nest defense scoring was adapted from studies on songbirds and raptors (Wiklund, 1990a; Kontiainen et al., 2009; Betini and Norris, 2012; Burtka and Grindstaff, 2013; Carrillo and González-Dávila, 2013; Møller and Nielsen, 2014). Observations of nest defense behavior outside the 2-minute focal observation were not counted towards scores.

1.2.5 Statistical Analysis

We conducted our statistical analyses in four steps. First, we validated our assessment of nest defense by verifying that the three traits measured during our standardized nest approaches correlated as expected if they were each representative of nest defense (see 'Nest defense scoring'). Second, we assessed state-dependence and long and short-term repeatability of nest defense (see 'State-dependence and repeatability of nest defense'). Third, we evaluated support for (dis-)assortative mating by nest defense behavior (see 'Dis-assortative mating'). Lastly, we assessed if nest defense predicted measures of reproductive success and fitness (see 'Fitness models').

Nest Defense Scoring

We scored three behaviors during nest defense tests for each parent: minimum distance to observer, number of stoops, and FID and used PCA (principal component analysis) to estimate the correlation among these variables. The PCA was implemented in R version 3.63 using the function *prcomp* (R Core Development Team, 2020). We included only tests in which the focal individual was tested for all three nest defense measurements (i.e., minimum distance to the observer, number of stoops, and FID) during a visit. All variables were scaled and centered since they were measured in different units. We calculated eigenvalues by squaring standard deviations that were extracted from PC1, PC2, and PC3. Lastly, we used PC (principal components) that had an eigenvalue > 1 and loadings (> 0.4) to interpret the correlation between nest defense variables (Budaev, 2010).

State-dependence and repeatability of nest defense

We used the R package lme4 to construct a univariate model (linear mixed effect model) to assess state dependence and estimate short- and long-term repeatability of nest defense behavior (Dingemanse and Dochtermann, 2013; Bates et al., 2014). Based on our PCA results (see below), we used 'Minimum Distance to the Observer' as our proxy for nest defense. Minimum distance values were multiplied by -1 so that the individuals that approached the observer more closely (i.e., had smaller minimum distance values), were given higher nest defense scores. Next, we added the new minimum value to all observations to render them positive, before log transforming to meet model assumptions of normality. Additionally, 'Nest Stage' is a labile state and served as our proxy for brood value and we predicted an increase in nest defense behavior with increasing nest stage. We expected females to respond more strongly than males to increasing nest stage, and we included an interaction between 'Nest Stage' and 'Sex', although the interaction was not significant. For model simplicity we included fixed effects of 'Nest Stage', 'Sex', and 'Year' but not the interaction. However, interpretation of the main effects was not affected by removal of the interaction. We included random effects of ‘ID’ and ‘ID_Series’. ‘ID’ represented an individual peregrine and their corresponding color-coded band number (N = 37 individuals) or in cases in which an individual was not banded we used their NestID (random ID given to each nest every year) and sex of the individual (N = 71 individuals). ‘ID Series’ represented an individual’s ‘ID’ plus the year of the study to form a series. This allowed us to calculate short-term repeatability using the formula $(V_{individual} + V_{indvidual\ series}) / (V_{individual} + V_{indvidual\ series} + V_{residual})$, and long-term repeatability using the formula $(V_{individual}) / (V_{individual} + V_{individual\ series} + V_{residual})$ (Araya-Ajoy et al., 2015). Where $V_{individual}$ is the variance explained by the individual, $V_{individual\ series}$ is the variance explained by the series, and $V_{residual}$ is the residual variance (Nakagawa and Schielzeth, 2010; Araya-Ajoy et al., 2015).

We assessed model fit visually by examination of residuals. We then used the package *arm* and the function *sim* to generate 1000 simulations of the posterior distribution of the model parameters (Gelman et al., 2020). We used the package *MCMCglmm to* extract 95% credible intervals (CrI) around the mode (β) of the estimated effect using the 1000 simulations of the model, which represents the uncertainty in our measurements (Gelman and Hill, 2006; Hadfield, 2010; Wasserstein and Lazar, 2016). We then used the mode (β) of estimated effects and 95% CrI to evaluate support for each effect and report Bayesian p-values (i.e., proportion of estimates that overlap zero) for estimates whose CrI overlap zero (Cumming and Finch 2005; Wasserstein and Lazar 2016). We describe effects and associated CrI that do not overlap between estimates, and are biased away from zero (i.e., CrI not overlapping with zero), as showing ‘strong support for an effect.’ CrI that were centered around zero (i.e., equal distribution of CrI on both sides of zero) with an estimated effect near zero were interpreted as showing ‘no support’ or ‘strong support for no effect.’ CrI that overlapped with zero but were not centered around zero (≤15% overlap) were interpreted as showing ‘moderate support’ for an effect since a Bayesian p-value of ≤0.15 corresponds to at least five times greater support for an interpretation of an effect than it does for the interpretation of no effect (Cumming, 2009). This form of interpretation presents the estimated effect and its likelihood and operates under the assumption that support for an effect (or the lack of support) can vary continuously (Cohen, 1994).

(Dis)-assortative mating

We used the R package MCMCglmm and constructed two bivariate models (generalized linear mixed-effect model using Markov Chain Monte Carlo simulations) to estimate (dis-

)assortative mating (Hadfield, 2010; Hadfield et al., 2019). Unlike other approaches which use the mean of repeated measurements, we chose to use a pair-level bivariate model since it uses all of the behavioral tests in which both parents were present during the two-minute focal observation. Using this method allowed us to estimate the within-pair residual correlation (i.e., shared labile environment) (Gelman and Hill, 2006; Hadfield, 2010; Class et al., 2017; Hadfield et al., 2019), in addition to the among-pair correlation (i.e., shared non-labile environment and/or (dis-)assortative mating). All the models were fit with a Gaussian error distribution and we log-transformed 'Minimum distance' values to meet assumptions of normality. We ran 2018 and 2019 separately, and used a bivariate prior specification that could account for one random effect (Class et al., 2017). We performed 590,000 iterations of each model with a thinning interval of 500 and a burn-in of 90,000 to achieve an effective sample size of 1000 simulations. We assessed model fit visually be inspecting trace and density plots. We calculated Bayesian p-values (i.e., the proportion of estimates that overlapped with zero) for estimates whose credible intervals overlapped with zero. We followed the same interpretations of intercepts and CrIs as presented in the 'Repeatability and state-dependence of nest defense' section (Gelman and Hill, 2006).

Fitness models

Finally, we evaluated whether nest defense predicted fitness proxies and measures of reproductive success (i.e., probability to hatch a nestling, probability of fledging a nestling, number of nestlings fledged, and nestling mass at fledging). We used a four-step approach: (1) we used all nests that initiated egg laying to estimate if nest defense predicted probability of hatching at least one nestling, (2) we used all nests that hatched at least one nestling to estimate if nest defense predicted the probability of fledging at least one nestling, (3) we used all nests that fledged at least one nestling to estimate if nest defense predicted the number of nestlings fledged, (4) we used all measurements of nestling mass at fledging (i.e., banding age) and centered them by sex to estimate if nest defense predicted nestling mass at fledging. We centered body mass within sex because peregrines are sexually dimorphic. In doing so, we removed effects of sex and sex ratio on brood biomass, and instead ask whether nest defense scores are associated with the production of nestlings that are relatively heavy (or light) for their sex.

To run these analyses, we used all individuals first nest defense test of the year as their nest defense score for that given year. We dropped nests that contained nest defense scores for only one adult out of the pair from the analysis. We used fixed effects of ' Year' and we include interactions between 'Year' (fitted as a factor) × 'Male nest defense' and 'Year' (fitted as a factor) × 'Female nest defense', and a random effect of 'SiteID' and 'NestID', and log-transformed and centered nest defense in both models. We then estimated the probability to hatch at least one nestling and fledge at least one nestling by fitting a binary (i.e., 0, 1) response variable and we used a binomial error distribution for both models. We used a Poisson error distribution for our model assessing number of nestlings fledged, and a Gaussian error distribution for our model assessing nestling mass at fledging. We verified that the binomial and Poisson models were not over-dispersed, and that the residuals were normally distributed for the Gaussian model. We followed the same method to obtain parameter estimates and interpretations of intercepts and CrIs as presented in the 'State-dependence and repeatability of nest defense' section above (Gelman and Hill, 2006).

1.3 Results

Nest Defense Scoring

After excluding tests that did not contain all three nest defense measures, we were left with 321 tests for the PCA. PC1 explained 44% of the variation in nest defense variables, while PC2 and PC3 explained 33% and 23% of the variation respectively. PC1 was the only component that had an eigenvalue above 1 (eigenvalue PC1: 1.3, PC2: 0.9, PC3: 0.7), thus we used PC1 for interpretation (Budaev, 2010). Number of stoops was heavily positively loaded and minimum distance to the observer was heavily negatively loaded on PC1. The loading of FID was < 0.4 thus we excluded it from interpretation (Budaev, 2010). From our PCA analysis, a high PC1 value was indicative of a peregrine that stooped more often and approached closer to the observer during the nest defense test and is consistent with aggressive nest defense behavior (see Table A.1). Although our PCA confirmed that number of stoops and minimum distance to the observer measured in our nest defense test were associated as predicted if each was an expression of nest defense, we nonetheless chose to use minimum approach distance in analyses going forward rather than PC1. This has several advantages, but most notably, that values are not contingent on the set of individuals being included in the analysis (as is the case with components extracted from PCA). Tests in which an individual was not present at the nest for the behavioral test are treated as missing values.

State-dependence and repeatability of nest defense

We conducted a total of 227 nest visits to score nest defense. Of these, there were 185 cases where at least one parent was present, for a total of 369 nest defense tests (218 female, 151 male). In 2018, 56 individuals were tested (29 females, 27 males), and in 2019, 67 individuals were tested (35 females, 32 males). There were 16 individuals (11 females, 5 males) that were tested in both seasons. Analyses of nest defense as a function of 'Sex', 'Nest Stage' and 'Year' found no significant difference between female (β = -1.29, 95% CrI = -1.45, -1.18) and male (β = -1.22, 95% CrI = -1.37, -1.10) nest defense behavior. We also found strong support that peregrines adjusted levels of nest defense behavior across nest stages (Table 1). Defense was highest during the provisioning stage (β = 0.30, 95% CrI = 0.18, 0.41) and lowest during egg laying (Table 1). We found strong support for an effect of 'Year' (β = -0.14, 95% CrI = -0.13, -0.16) with lower defense scores occurring in 2019 compared to 2018. We found strong support for moderate short-term repeatability (i.e., within-year) (r = 0.37, 95% CrI = 0.32, 0.41), and long-term repeatability (i.e., between-year) repeatability (r = 0.19, 95% CrI = 0.16, 0.24) of nest defense behavior. Long-term repeatability was significantly lower than short-term repeatability (i.e., 95% CrI were non-overlapping).

(Dis)-assortative mating

We had 148 unique pair-level tests (2018 = 75 tests, 2019 = 73 tests) at 57 nests (2018 = 27 nests, 2019 = 30 nests) for which both the male and female were present during nest defense observations. We found moderate support for assortative mating among-pairs (β = 0.34, 95% CrI = -0.29, 0.72, Bayesian p-value = 0.15), and weak support for a positive within-pair correlation (β = 0.14, 95% CrI = -0.16, 0.36, Bayesian p-value = 0.24) in 2018. In contrast, in 2019, we found strong support for disassortative mating among-pairs (β = -0.54, 95% CrI = -0.82, -0.02) and strong support for a positive within-pair correlation (β = 0.40, 95% CrI = 0.21, 0.63).

Fitness models

First, we evaluated the probability to hatch at least one nestling. We used the first test of a given year as an individual's aggression score for that year, which left us with n = 112 individuals at n = 27 nests in 2018 and n = 29 nests in 2019. We found no support for differences in hatching probabilities across years since the 95% CrI for each year overlapped by greater than 15% (Table 2). We found strong support that more defensive females (β = 3.50, 95% CrI = 0.29, 8.99) and moderate support for defensive males (β = 1.15, 95% CrI = -0.59, 3.28, Bayesian p-value = 0.11) having a higher probability of hatching at least one nestling in 2018. Additionally, in 2019 we found moderate support for a positive association between nest defense scores in females and the probability of hatching at least one nestling (β = 0.93, 95% CrI = -0.44, 2.28, Bayesian p-value = 0.14). We found no support for an effect of male defense on hatching probability in 2019 since the CrI were centered around zero and the effect size was near zero (Table 2).

Next, we excluded nests that did not hatch at least one nestling to assess, among- nests that hatched at least one nestling, whether nest defense predicted the probability of fledging a nestling. These analyses were conducted on n = 74 individuals at n = 19 nests in 2018 and n = 18 nests in 2019. We found a higher probability of fledging a nestling in 2018 (β = 1.76, 95% CrI = -0.06, 3.46) compared to 2019 (β = -1.19, 95% CrI = -2.34, 0.08), and this difference was significant (β = -3.18, 95% CrI = -4.91, -0.69). We found moderate support that higher levels of nest defense in males (β = -1.72, 95% CrI = -4.42, 0.70, Bayesian p-value = 0.06) was associated with a lower probability of fledging a nestling in 2018. We found no support for female nest defense to be associated with fledging probabilities in 2018 (β = -0.46, 95% CrI = -5.32, 2.58, Bayesian p-value = 0.20). The opposite was true for 2019, with moderate support for higher levels of male defense associated with higher probability of fledging a nestling (β = 1.74, 95% CrI = -0.40, 3.53, Bayesian p-value = 0.05). There was no support for an effect of female nest defense on fledging probability (β = 0.69, 95% CrI = -1.29, 1.76, Bayesian p-value = 0.40). Next, we assessed if nest defense predicted the number of nestlings fledged for nests that fledged at least one nestling or more (n = 13 nests in 2018, n = 5 nests in 2019). We found strong support for more nestlings fledged in 2018 (β = 0.74, 95% CrI = 0.26 1.04) compared to 2019 (β = 0.28, 95% CrI = -0.61, 1.11), and no support for male or female nest defense to impact the number of nestling fledged in both years since effect sizes were near zero and CrI centered around zero (Table 2).

Lastly, we assessed if nest defense predicted nestling mass at fledging. We had a total of n = 32 nestlings fledged (n = 25 in 2018, n = 7 in 2019) at n = 19 nests (n = 13 in 2018, n = 5 in 2019). Nestlings fledged were in better condition in 2018 (β = 5.30, 95% CrI = -29.46, 37.86) compared with 2019 (β = -31.59, 95% CrI = -105.18, 33.76), and there was moderate support for an overall effect of year (β = -38.11, 95% CrI = -119.83, 36.66, Bayesian p-value = 0.14). Additionally, we found a tendency for more defensive males to produce nestlings in better condition in 2018 (β = 36.93, 95% CrI = -43.78, 87.90, Bayesian p-value = 0.21) but this was not significant. In addition, we found moderate support for more defensive males to produce nestlings in better condition in 2019 (β = 34.79, 95% CrI = -42.42, 131.92, Bayesian p-value

0.15). The opposite was true for females, we found a tendency that more defensive females produced nestlings in worse condition in 2018 (β = -63.74, 95% CrI = -187.02, 59.42, Bayesian p-value = 0.21) but this was not significant. In 2019 we found moderate support (β = -48.43, 95% CrI = -122.71, 19.85, Bayesian p-value = 0.07) for more defensive females to produce nestlings in worse condition.

1.4 Discussion

We evaluated support for three mechanisms that have been proposed to contribute to the maintenance of among-individual differences in nest defense behavior: state-dependence, assortative mating, and fluctuating selection. We found that nest defense behavior was repeatable in peregrine falcons both within and between years. Peregrines adjusted their nest defense in response to nesting stage and year, revealing plastic adjustment of nest defense. We also found evidence for assortative mating and fitness consequences, but these differed between years. In 2018, there was moderate support for assortative mating by nest defense score, and higher defense levels in both males and females was associated with lower reproductive success. In contrast, in 2019, there was strong evidence of disassortative mating, but for both males and females, higher nest defense scores were associated with greater reproductive success. We discuss these results in the context of how temporal variation in the environment may influence selection on defensive and non-defensive behavioral types.

Both male and female peregrine falcons invest into nest defense as a form of parental care and we found repeatable differences in how peregrines invest in this form of parental care. In our study population, minimum approach distances ranged from 0 m (i.e., hit or near miss of observer) to 600 m, and individuals differed consistently in this measure of nest defense over both the short- (r = 0.37) and long-term (r = 0.19). The repeatability of nest defense has been studied in at least 3 other raptors, which similarly found both short- and long-term repeatability (Kontiainen et al., 2009; Møller and Nielsen, 2014; Arroyo et al., 2017). Peregrines are reversed sexual size dimorphic, with females being larger than males and therefore, females are often considered to be the primary nest defenders (Wiklund and Stigh, 1983; Andersson and Wiklund, 1987; Wiklund, 1990a). Surprisingly, in our population we found no difference between male and female nest defense (Table 1). Our findings of similar nest defense scores in males and females contrasts with other raptors which have higher investment by females (Galeotti et al., 2000; Kontiainen et al., 2009; Møller and Nielsen, 2014; Arroyo et al., 2017). We suggest that the similar levels of nest defense in male and female peregrines may be due to a more equivalent allocation of parental care duties compared to other raptor species.

We also found that nest defense increased (i.e., individuals stooped closer to observer on average) as a function of nest stage with the closest distances occurring during the provisioning stage and the furthest distances during egg laying (Table 1). Our bivariate analysis, which found a positive within-pair correlation (i.e., shared environment effect) in both study years, also revealed that peregrines undergo state-dependent adjustments in nest defense behavior, and that males and females are adjusting to changes in their shared labile environment. This pattern of increasing nest defense with nest stage progression occurred in both sexes and in both study years, and likely reflects the change in optimal parental investment with nest stage progression. The breeding season in the Arctic is a short window and there is low opportunity for re-nesting once a pair has progressed significantly into the breeding season (Cade, 1960; Falk et al., 1986; Poole and Bromley, 1988; Bradley et al., 1997). Peregrines breeding in Rankin Inlet have a narrow range of laying dates (~12 days; Bradley et al., 1997), to successfully produce nestlings before the seasonal decline in resources, compared to other northern populations in central Canadian arctic (~18 days; Poole and Bromley, 1988), Alaska (~21 days; Cade, 1960), southern Greenland (~30 days; Falk et al., 1986), and more tropical regions like Australia (~45 days; Olsen and Olsen, 1989). Increased nest defense over the nesting stage likely reflects the increased chance of fledging a nestling while simultaneously reflecting the low prospective for re-nesting. Similar patterns of increasing nest defense with advancing nest stage has been observed in numerous songbirds (Greig-Smith, 1980; Curio, 1987; Westneat, 1989; Rytkönen et al., 1990; Svagelj et al., 2012) and raptors (Biermann and Robertson, 1981; Sproat and Ritchison, 1993; Galeotti et al., 2000; Sergio et al., 2001), and is accordance with assumptions that nestlings are more valuable than eggs, and consequently, merit greater parental investment (Trivers, 1972; Montgomerie and Weatherhead, 1988).

We also evaluated support for (dis)assortative mating, which has been documented in several other avian species (Both et al., 2005; Schuett et al., 2011; Gabriel and Black, 2012; Burtka and Grindstaff, 2015). Unexpectedly, we found evidence for assortative mating in 2018 and disassortative mating in 2019. Pairs that mated assortatively and were the most defensive had a lower chance of fledging a nestling in 2018. In 2019, pairs mated disassoratively and higher nest defense in both males and females was associated with a higher probability of successfully fledging a nestling. Similarly, Both et al. (2005) found evidence for assortative and disassortative mating by exploratory behavior in the same Great tit population within a 3-year period, and the fitness benefit fluctuated between years. We hypothesize that mate choice in peregrine falcons is dependent upon environmental conditions that regulates how behavioral types are valued. If environmental conditions dictate mate choice, females could be selecting for indirect benefits such as an optimal male behavioral type for the current ecological context (e.g., high resources, low resources; high frequency of heavy rain events, low frequency of heavy rain events) in which adaptive traits or an intermediate behavioral type would then be passed on to her offspring (Munson et al., 2020).

Alternatively, females could be assessing male behavioral types during courtship to determine his ability to provide direct benefits such as parental care. Aggressive nest defense behavior in males could carry over into other contexts, such as courtship behavior forming a behavioral syndrome (i.e. correlation of multiple traits). Although, aggressive male behavior in courtship would be strictly tied to agonistic interactions with other males since females are dominant over males. Accordingly, in poor years when food availability is low females could be selecting for direct benefits that are related to food acquisition and use cues, such as aggressive behavior during courtship or any other trait that covaries with aggressiveness, to determine their partner's ability to provision offspring, which has been found to both positively (Wetzel and Westneat, 2014) and negatively covary (Mutzel et al., 2013; Wischhoff et al., 2018) with nest defense. We cannot rule out that more reliable cues exist that convey high provisioning ability, such as carotenoid-dependent colorations of bare parts (i.e., cere, lore, legs, feet) or plumage. In peregrines, male bare parts become more vibrant during the breeding season and could provide a reliable cue to females about the quality of the male, specifically his provisioning and foraging ability (Vergara and Fargallo, 2011; Garcia-Navas et al., 2012; Iverson and Karubian, 2017). However, the fact that breeding adults mated assortatively in one year, and disassortatively in the other, reveals that the stable among-individual differences in nest defense observed in this study cannot be explained by shared stable environmental differences among-pairs and are at least partially due to among-individual differences in state.

Finally, we explored the consequences of among-individual differences in nest defense behavior on reproductive success. We found that 2018 and 2019 were markedly different years in terms of reproductive success and weather. Weather conditions obtained from Environment and Climate Change Canada (2021) website, in Rankin Inlet during July and August (i.e., critical hatching and nestling rearing phases) was considerably different from

2018 to 2019. During the 2018 season Rankin Inlet received fewer heavy rain events (i.e., precipitation events ≥ 8 mm/day; Anctil et al., 2014), that are known to cause nestling mortality in our population, and less total precipitation (July = 15.8 mm, 0 heavy rain events; August = 52.8 mm, 1 heavy rain event) compared to 2019 (July = 112.8 mm, 6 heavy rain events; August = 112.9 mm, 5 heavy rain events). At the population level a year with less heavy rain events (2018) translated into a higher probability of fledging nestlings, more nestlings fledged, and nestlings with higher masses at fledging compared to 2019. Additionally, we found in both years that female nest defense was positively associated with the probability of hatching at least one nestling, although the strongest effect was found in 2018. We did find evidence for more defensive males having higher hatching probabilities in 2018 but there was no effect in 2019 (Table 2). Higher hatching probabilities found in more defensive females is likely attributed to the overall importance of female nest defense during the egg-laying and incubation phases to ward of potential nest predators such as Arctic foxes, wolverines, or short-tailed weasels.

We also found that nest defense influenced reproductive success, but the direction of the relationship varied between years. In 2018, more defensive individuals were less likely to fledge at least one nestling, and in 2019 the opposite was found and more defensive individuals were more likely to fledge at least one nestling. In both years, the patterns were the same for both males and females, indicating that selection acted on male and female nest defense in the same way within-years, though in 2018 less aggressive nest defense was favored and in 2019 more aggressive nest defense was favored. Our results add to the growing number of studies suggesting that fluctuating selection may be an important mechanism contributing to the maintenance of among-individual differences in behaviors (Dingemanse et al., 2004; Boon et al., 2007; Bergeron et al., 2013; Montiglio et al., 2014; Le Cœur et al., 2015; Nicolaus et al., 2016). For example, Nicolaus et al. (2016) found the maintenance of exploratory behavior was attributed to temporal fluctuations in the density of great tits with selection favoring slow explorers in high densities and fast explorers in low densities. Further work is needed to identify the ecological context (i.e., density, food availability, weather conditions) that could explain the apparent evidence for temporal variation in the environment acting on the selection of behavioral types in peregrines. However, studies in other species of birds and mammals have found that food availability (Dingemanse et al., 2004; Boon et al., 2007; Montiglio et al., 2014; Le Cœur et al., 2015) and density (Nicolaus et al., 2016) are key factors associated with fluctuating selection. For example, Le Cœur et al. (2015), found that shy individuals were favored in years with high resources (mast years) and bold individuals were favored in years with low resources. Similarly, we speculate that since peregrines in Rankin Inlet are exposed to an environment that temporally fluctuates between years of high and low food abundance (i.e., microtine cycles; Bradley et al., 1997), they could be under similar selection pressures documented by Dingemanse et al. (2004), and Le Cœur et al. (2015), in which a behavioral type is less successful in years with high resource availability and more successful during years with low resources and vice versa. In addition, breeding density fluctuations could also be associated with our findings of fluctuating selection. Although, we only have two years to compare, we observed fluctuations in the number of breeding pairs between years (2018 n = 28 breeding pairs, 2019 n = 34 breeding pairs) with high nest defense behavioral types doing better in high density years and low nest defense behavioral types doing better in lower density years. If nest defense is related to overall aggression, we could attribute this to more aggressive behavioral types being better at retaining high quality territories in high density years when competition is high, while in low density years aggression could be costly since competition is relaxed. Similarly, a feedback loop has been proposed between aggressiveness and population density, whereby changes in aggressive phenotypes triggered by natural selection can influence population density, thus resulting in differential selection for behavioral types that do best under different population densities (Mougeot et al., 2003; Duckworth, 2008; Duckworth and Aguillon, 2015).

Weather conditions could also influence the relationship between nest defense and fitness via an association between nest defense and provisioning (e.g., Betini and Norris, 2012). For example, if more aggressive nest defenders are more responsive to variation in offspring need as shown in other species (Betini and Norris, 2012), they may outperform less aggressive nest defenders when weather conditions are more challenging. Year-specific weather conditions are consistent with this idea with 2019 (n = 7 nestlings fledged; 11 heavy rain events) being a harsh year compared to 2018 (n= 25 nestlings fledged; 1 heavy rain events). We found that more defensive males in both years produced nestlings with a higher mass at fledging compared to the sex-specific population mean. The opposite effect was found in females, with more defensive females in both years producing nestlings with lower mass at fledging. We could attribute nestlings being fledged in better condition to more defensive males that engage in nest defense more often since they are of higher quality and can provide high levels of multiple parental care behaviors (i.e., nest defense and provisioning). Although, aggressive male nest defense corresponded with a lower probability of fledging a nestling in 2018 which suggests that a trade-off could exist for individuals that are not able to express high levels of multiple parental care traits. Alternatively, parental investment theory suggests that offspring that are in good condition (i.e., provisioned more frequently) should also be defended more thus our results could reflect a male’s response to a high brood value (Trivers, 1972; Montgomerie and Weatherhead, 1988). Future work should evaluate the proposed relationship between nest defense and provisioning behavior.

Conclusion

We studied the causes and consequences of variation in nest defense in Arctic peregrine falcons. Both male and female peregrines increased their level of nest defense with progression through the nest stage, indicating plastic response to shared labile-environment. However, we also observed repeatable among-individual variation in aggression with within- and across-years. We found some evidence that these differences were due to more than simply shared environment, because we only observed apparent assortative mating in one year, while in the other, there was strong evidence for disassortative mating. However, we also found support for fluctuating selection acting on behavioral types. We suggest that nest defense may be valued in years with high inter-specific competition and/or low food availability, potentially due to an inherent trade-off with other fitness relevant traits, such as provisioning. We recommend that future work should assess whether nest defense behavior trades-off with other parental care behaviors such as provisioning behavior, and whether this provides a mechanism for the fluctuating selection documented here.

1.5 Tables and Figures

Table 1. Univariate results of long and short-term repeatability of nest defense. The effect size estimates (β), and their 95% credible intervals (CrI) are reported. Significant fixed effects are in bold.

	Nest defense Log(minimum distance to observer)
Fixed effects	β (95% CI)
Sex	
Female	**-1.29 (-1.45, -1.18)**
Male	**-1.22 (-1.37, -1.10)**
Nest Stage	
Incubation	**0.17 (0.04, 0.27)**
Provisioning	**0.30 (0.18, 0.41)**
Year	**-0.14 (-0.27, -0.02)**
Random Effects	σ (95% CI)
Individual	0.04 (0.03, 0.06)
Individual Series	0.04 (0.03, 0.05)
Residual	0.14 (0.13, 0.16)
Repeatability	r (95%CI)
Short-term repeatability	0.37 (0.32, 0.41)
Long-term repeatability	0.19 (0.16, 0.24)

Table 2. Results from models assessing if nest defense predicts probability of hatching at least one nestling, probability of fledging at least one nestling, number of nestlings fledged, and nestling mass at fledging. The effect size estimates (β), and their 95% credible intervals (CrI) are reported. Estimates in bold are 'strongly supported', estimates with an Asterix are 'moderately supported.'

	Measures of reproductive success and fitness			
	Probability of hatching at least one nestling	**Probability of fledging at least one nestling**	**Number of nestling fledged**	**Nestling mass at fledging**
Fixed effects	**β (95% CrI)**	**β (95% CrI)**	**β (95% CrI)**	**β (95% CrI)**
Year				
2018	0.72 * (-0.36, 1.55)	1.76 * (-0.06, 3.46)	**0.74 (0.26, 1.04)**	5.30* (-29.46, 37.86)
2019	0.64 * (-0.25, 1.38)	-1.19 * (-2.34, 0.08)	0.28 (-0.61, 1.11)	-31.59 * (-105.18, 33.76)
ND × Year				
Male_ND × 2018	1.15 * (-0.59, 3.28)	-1.72 * (-4.42, 0.70)	0.17 (-0.70, 1.09)	36.93 (-43.78, 87.90)
Male_ND × 2019	0.14 (-1.03, 1.33)	1.74 * (-0.40, 3.53)	-0.10 (-0.87, 1.67)	34.79 * (-42.42, 131.92)
Female_ND × 2018	**3.50 (0.29, 8.99)**	-0.46 (-5.32, 2.58)	0.10 (-1.40, 1.64)	-63.74 (-187.02, 59.42)
Female_ND × 2019	0.93 * (-0.44, 2.28)	0.69 (-1.29, 1.76)	-0.06 (-0.89, 0.83)	-48.43 * (-122.71, 19.85)
Random Effects	**σ (95% CrI)**	**σ (95% CrI)**	**σ (95% CrI)**	**σ (95% CrI)**
NestID	0.00 (0.00, 0.00)[1]	0.00 (0.00, 0.00)[1]	0.00 (0.00, 0.00)[1]	730.83 (302.69, 1783.21)
Residual	1	1	1	4096.35 (2563.91, 8100.06)

1. Nest ID variance was non-estimable.

Figure 1. Raw minimum distance values. Lower minimum distance values equates to higher nest defense levels and vice versa. Figure depicts state-dependent adjustments of nest defense behavior. Nest defense increases from egg-laying through provisioning stages in both years. Note, males and females are not presented separately as there was no support for an interaction between sex and nest stage on aggression (see main text).

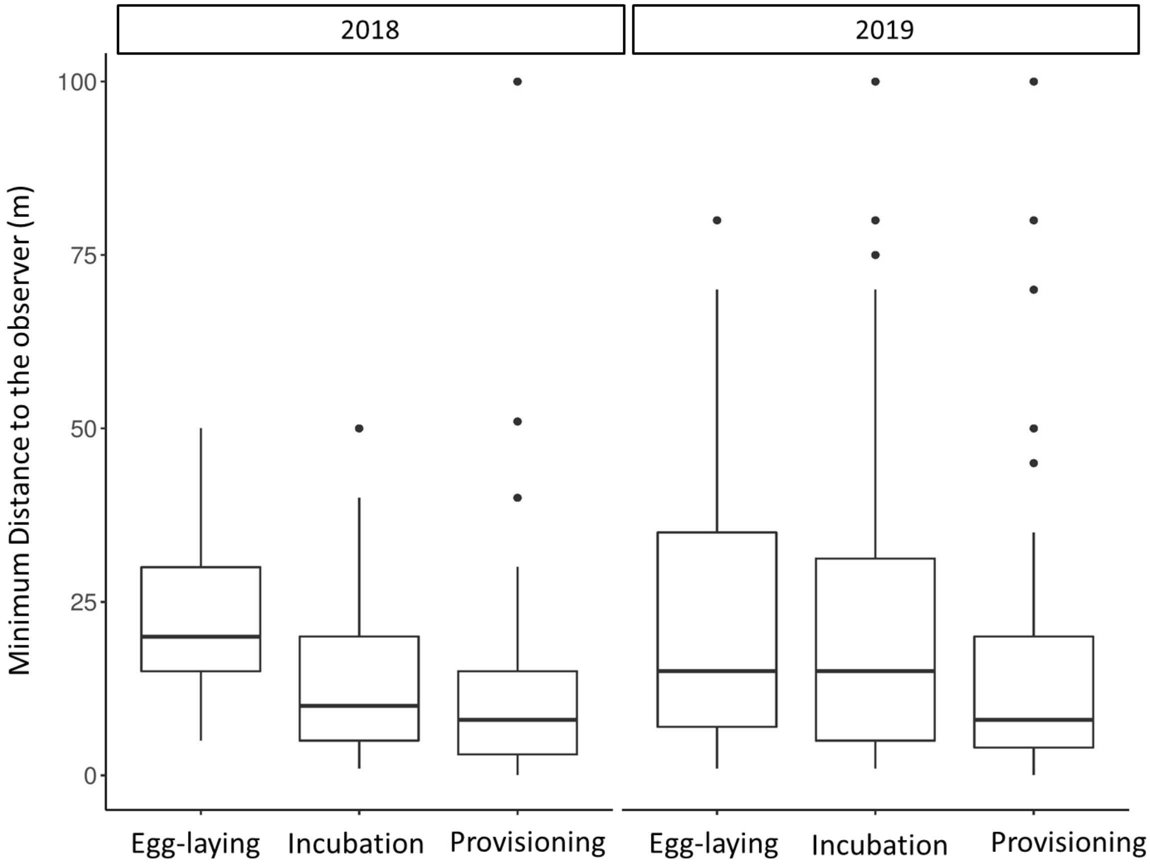


Figure 2. Within and between nest effects. Raw 'Minimum Distance' values were log-transformed and within (C, D) and between (A, B) subject centered. Positive 'Minimum Distance' values are equated to high nest defense scores and negative 'Minimum Distance' values are equated to low nest defense scores. Panel A and B depict the between-nest covariance. Panel A shows evidence for positive assortative mating (i.e., similar personalities are paired) in 2018, while Panel B shows evidence for (dis-) assortative mating (i.e., dissimilar personalities are paired) in 2019. Panel C and D, depict the within-nest covariance (i.e., shared environmental effect). Panels D show evidence for a positive shared environmental effect in 2019.

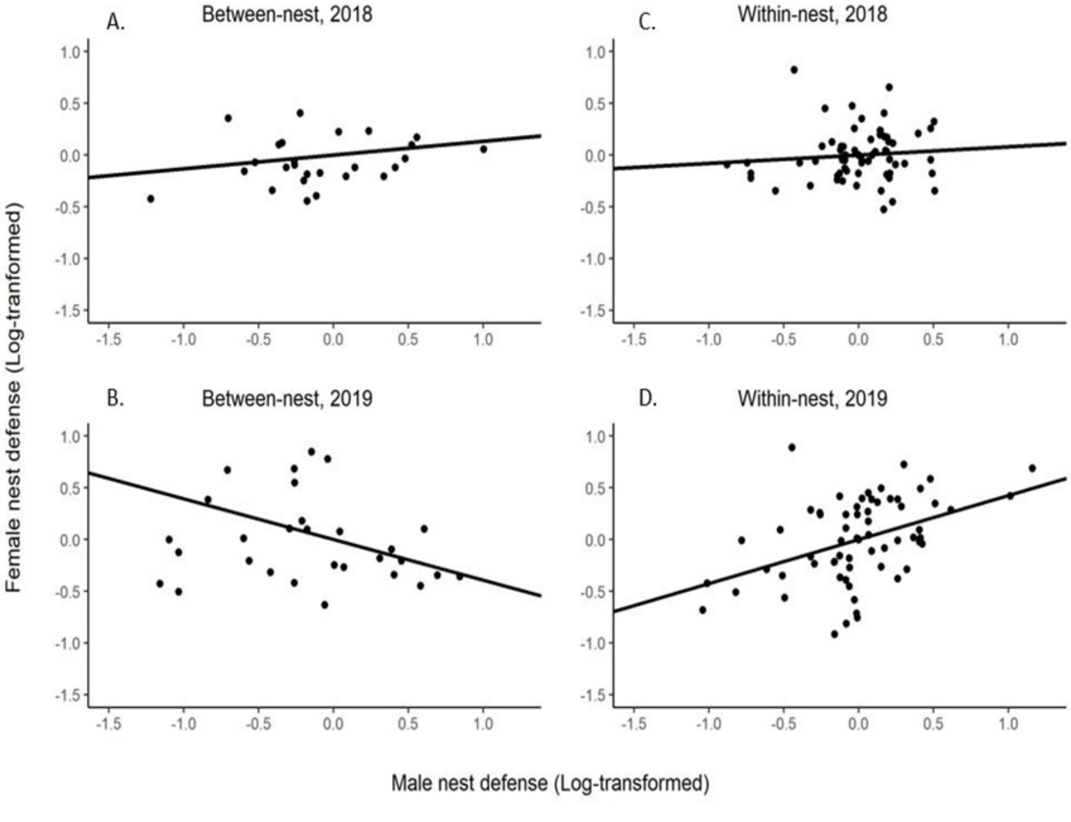
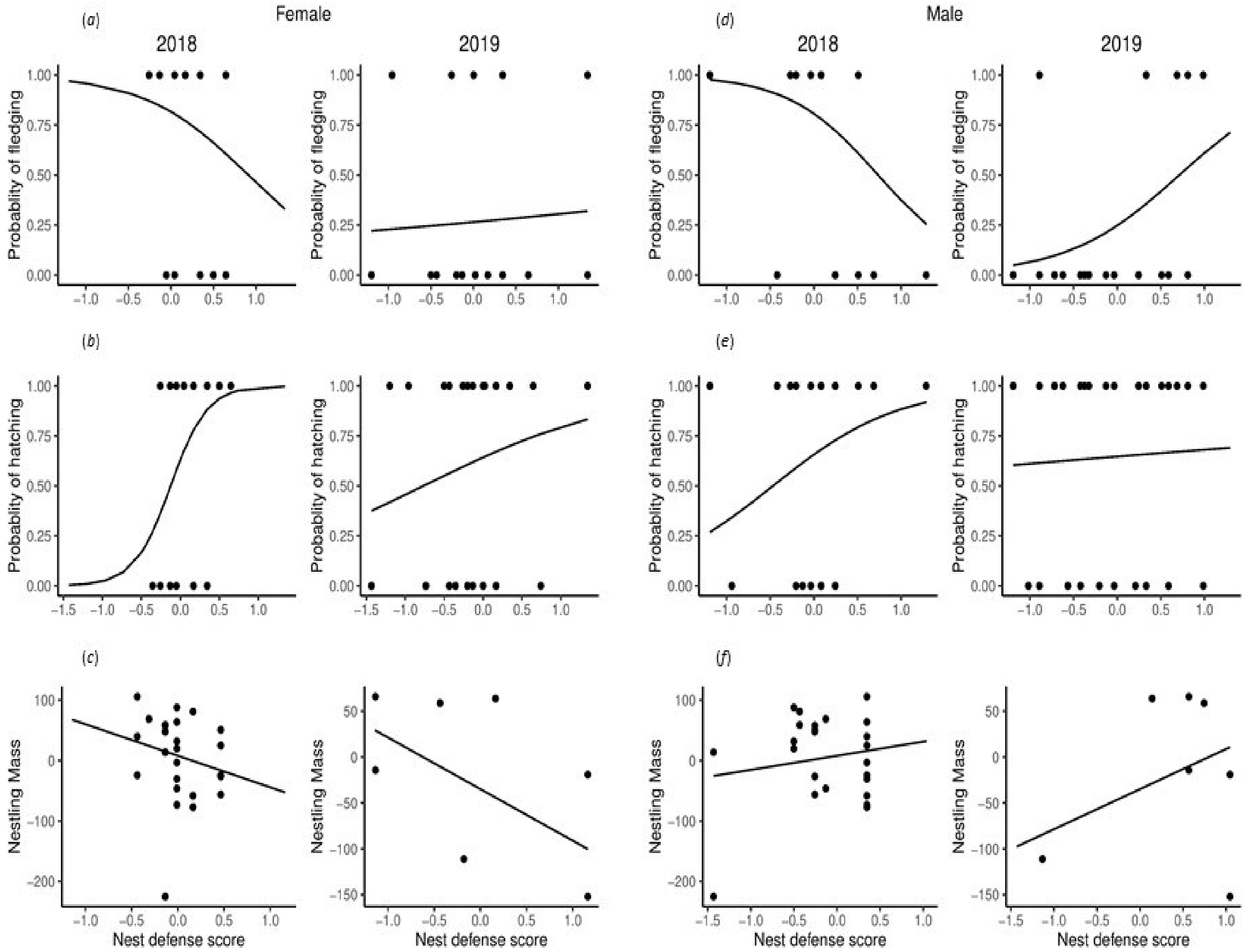


Figure 3. Fluctuating selection acting on behavioral types. Raw ‘Minimum Distance’ values were log-transformed and centered. Higher nest defense scores equated to individuals being more defensive. Probability of fledging at least one nestling in relation to nest defense score in females (*a*) and males (*d*). Probability of hatching at least one nestling in females (*b*) and males (*e*). Nestling mass at fledging in relation to female (*c*) and male (*f*) nest defense.



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Appendix

A.1 PCA Output

Table A.1. Results from PCA on measures of nest defense. Significant loadings and eigenvalues are in bold.

Measures of nest defense (loadings)	**PC1**	**PC2**	**PC3**
FID (Flight initiation distance)	0.35	-0.88	-0.29
Stoops	**0.69**	0.03	0.71
Minimum distance	**-0.62**	-0.46	0.63
Proportion of Variance	0.44	0.33	0.24
Eigenvalue	**1.3**	0.98	0.70

A.2 PCA Plot

Figure A.2. Results from PCA of nest defense measures. Minimum distance and dive correlated as expected with peregrines that stooped more often also dove closer to the observer.