**Fluctuating selection on nest defense behavior in Arctic peregrine falcons (*Falco peregrinus tundrius*)**

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**Data Accessibility Statement**

All r-scripts and data required to replicate the analyses presented in this manuscript are available on the Open Science Framework digital repository (<https://osf.io/euk4s/>).

**ABSTRACT**

**Keywords**:

**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 aggression (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 aggression 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, a; 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 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, 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 aggression and 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) such as sex, offer a simple explanation for among-individual differences since the state 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 aggressive 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, has been shown to 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 result is consistent with parental investment theory (i.e., PI) 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 chicks 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, many of the labile state characters known to influence nest defense have been shown to 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 have higher success. This 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 aggressiveness 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 behavioural 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). Previous 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 behavioural variation was attributed to fluctuating food availability, with fast exploring males having lower fitness in years with peak beech 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).* 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 (dis-)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 (dis-)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 nest productivity and fitness by using the first nest defense test of the year to quantify the effects on various fitness proxies (i.e., probability of fledging, number fledged, and average 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.

**METHODS**

*Study species*

Arctic peregrine falcons are long-distance migrants that winter in Central and South America and breed in the Canadian Arctic (Court et al., 1988). Peregrines arrive to 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), though nests of 5 eggs have been observed on occasion at our study site (NAG personal observation). The incubation period lasts approximately 33.5 days (Burnham, 1983), 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).

In most raptor species, males specialize in hunting prey for the nest and females incubate, brood, and partition prey items into smaller morsels acting as a food processor for nestlings (Enderson, 1973; Sonerud, 1992; Palmer et al., 2001; Slagsvold and Sonerud, 2007; Sonerud et al., 2014a; Sonerud et al., 2014b). Raptors are single prey loaders that capture large prey items which take longer to ingest by offspring and require considerable handling time by females at the nest (Sonerud, 1992; Slagsvold and A. Sonerud, 2007; Sonerud et al., 2014a; Sonerud et al., 2014b). Since females are constrained to the nest, providing other parental care duties, and better able to defend the nest due to their larger body size (Andersson and Åke, 1981), it would pay for males to invest more into hunting rather than defending.

*Study site*

This study was carried out in a 455 km² area around Rankin Inlet, Nunavut (62°49′N, 92°05′W). The community ofRankin Inlet is situated on the western coast of Hudson Bay. Most of the study area is encompassed within Hudson Bay which is dominated by a rugged coastline that provides numerous suitable cliffs for cliff-nesting species such as peregrine falcons, rough- legged hawks, 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 (*Spermophilus parryii*), shorebirds, songbirds, waterfowl, and seabird colonies.

Arctic peregrine falcon breeding in Rankin Inlet, Nunavut, Canada have been studied since the 1980s to better understand the ecology and toxicology following the widespread decline of peregrines from DDT (Court et al., 1988; Franke et al., 2010). 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). Peregrines in Rankin consume an unusually high amount of mammalian prey in their diet compared to other study sites around the world, but they still rely heavily on avian prey and are considered a generalist top predator (Bradley and Oliphant, 1991; Franke et al., 2010)

*Fieldwork*

Fieldwork began in mid-May for both 2018 and 2019 seasons. This corresponded with the arrival of peregrines to Rankin Inlet from their annual migration from their southerly wintering grounds. A full census of the study area was conducted at least twice per field season using snowmobiles to determine occupancy. Occupancy was determined based on presence of territorial adults, evidence of scrape excavation, or discovery of a nest with eggs (following Franke et al., 2010). A site was determined to be unoccupied if the breeding season had progressed significantly (i.e., four weeks after first nests were initiated in the study area) and the site was still vacant (Franke et al., 2010). Once eggs were detected, we deployed RECONYX motion-activated cameras at the nesting site (i.e., 2018: n = 28, 2019: n = 34). Active nests were visited every 6-7 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 that were on adults. Once chicks hatched, a non-toxic color was applied to one leg to track growth until fledging (Court et al., 1988; Anctil et al., 2014). A chick was considered fledged once it had reached ~20 days old. We did not conduct nest visits after ~20 days to avoid inducing early fledging. Chicks that had fledged were fitted with a U.S. Fish and Wildlife band (Court et al., 1988; Franke et al., 2010).

*Nest defense tests*

Nest defense tests occur during egg laying, incubation, and provisioning stages of the nesting cycle. For each visit, we record nest site ID, date, observer, travel mode (i.e., helicopter, snowmobile, quad, or boat), nest approach direction (from above or below), and time of day. Nests can be approached from above or below the actual nesting site depending on the orientation and accessibility of the cliff. Studies of other cliff-nesting species have documented that the perceived threat of nest intruders varies depending on the approach (i.e., above or below) (Fernandez, 1993; Beardsell et al., 2016; Natusch et al., 2017). We recorded nest approach direction to allow us to control for this potential effect. We also documented approach method (e.g., boat, helicopter, snowmobile, or quad) to account for potential differences in nest defense caused by differences in the level of noise and disturbance generated by different approach methods. 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). FID is a widely used metric of nest defense 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. During this time, the observer recorded the number of dives 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, one to monitor each parent. Assignment of observers to parents was done haphazardly for each test. After the focal observation, birds were assigned a nest defense score on a 0-5 scale: 0— bird is not present, 1— bird is present but not vocalizing, 2— bird is calling but not in flight, 3— bird is circling overhead with or without vocalizations, 4— stooping/diving toward observer, 5—hitting or near miss of the observer. Methods for nest defense scoring are adapted from various 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.

*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 are each representative of nest defense (see ‘Aggression scoring’). Second, we assessed state-dependence and long and short-term repeatability of nest defense (see ‘State-dependence and repeatability of aggression’). Third, we evaluated support for (dis-)assortative mating by aggressiveness (see ‘Dis-assortative mating’). Lastly, we assessed if nest defense predicted measures of fitness (see ‘Fitness models’).

*Aggression scoring*

We scored three behaviors during nest defense assays for each parent: minimum distance to observer, number of dives, and FID (see above for descriptions) and used PCA (principal component analysis) to understand the correlation between these variables. The PCA was constructed in R version 3.63 using the function *prcomp* (R Core Development Team, 2020). We included only tests in which the focal individual was assayed for all three nest defense measurements (i.e., minimum distance to the observer, number of dives, 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 of greater than 1 and loadings ( > 0.4) to interpret the correlation between aggression variables (Budaev, 2010).

*State-dependence and repeatability of aggression*

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 chose to use ‘Minimum Distance to the Observer’ as our proxy for aggression. Minimum distance was log transformed to meet model assumptions of normality. We included fixed effects of ‘Nest Stage’, ‘Sex’, and ‘Year.’ Since we expected both sexes to respond similarly to increasing nesting stages, we did not include an interaction between ‘Nest Stage’ and ‘Sex’. We included random effects of ‘ID’ and ‘ID\_Series’. Whereas ‘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 (Vindividual + Vindvidual series) / (Vindividual + Vindvidual series + Vresidual), and long-term repeatability using the formula (Vindividual ) / (Vindividual + Vindividual series + Vresidual) (Araya-Ajoy et al., 2015). Where Vindividual  is the variance explained by the individual, Vindividual series is the variance explained by the series, and Vresidual 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 to obtain parameter estimates (Gelman et al., 2020). We used the package *MCMCglmm to* extract 95% credible intervals (CI) around the mean (β) using the 1000 iterations of the model, which represents the uncertainty in our measurements (Gelman and Hill, 2006; Hadfield, 2010). 95% credible intervals are comparable to a frequentist p-value of p ≤ 0.05 when the null hypothesis occurs outside the limits of the CI. The support for effects was based on parameter estimates obtained from the posterior distribution and their corresponding 95% CI (Gelman and Hill, 2006). We describe effects that overlap with zero but are not centered around zero as showing ‘moderate support’, and effects that did not overlap zero as showing ‘strong support’ (Cumming, 2009). Estimates that were centered around zero are described as showing ‘no support’ for an effect, or ‘strong support’ for lack of an effect.

*(Dis-)assortative mating*

We used the R package MCMCglmm and constructed two pair-level 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 (i.e., controlling for no within-pair correlation), we chose to use a pair-level bivariate model since it uses all of the behavioral tests in which both parents are 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 subset years and ran ‘2018’ and ‘2019’ independent of each other 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 burnin 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., proportion of estimates that overlap with zero) for intercepts whose credible intervals overlapped with zero. We followed the same interpretations of intercepts and CIs as presented in the ‘Repeatability and state-dependence’ section (Gelman and Hill, 2006).

*Fitness models*

Finally, we evaluated whether nest defense predicted measures of fitness (i.e., probability to fledge one chick, number of chicks fledged for nests that fledged one chick or more, and average chick mass at fledging).We used a three-step approach (1) We estimated the probability to successfully fledge a chick for all nests (2018 n = 30 nests, 2019 n = 34 nests), (2) we used all nests that were successful in fledging at least one chick (2018 n = 14 nests, 2019 n = 5 nests) to estimate if aggression predicted the number of chicks fledged, and (3) we used all nests that fledged chicks (2018 n = 14 nests, 2019 n = 5 nests) and calculated the average mass of chicks fledged at each nest to estimate if aggression predicted chick mass at fledging. To do this, we used all individuals first nest defense test of the year as their aggression score for that given year. We used fixed effects ‘Sex’ × ‘Year’ (fitted as a factor) × ‘Aggression’, and a random effect of ‘SiteID’, and log-transformed aggression in both models to meet assumptions of normality. We then estimated the probability to successfully fledge a chick by fitting binary (i.e., 0, 1) response variable and we used a binomial error distribution. We used a Gaussian error distribution for our model assessing the number of chicks fledged and chick mass at fledging, and assessed model fit visually by inspection of residuals. We followed the same method to obtain parameter estimates and interpretations of intercepts and CIs as presented in the ‘State-dependence and repeatability of aggression’ section above (Gelman and Hill, 2006).

**RESULTS**

*Aggression 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 variance in aggression variables, while PC2 and PC3 explained 33% and 23% of the variance 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 dives 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 dove more often and approached closer to the observer during the nest defense test and is consistent with high aggression (see ESM Table S1). Although our PCA confirmed that number of dives and minimum approach distance 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 assay are treated as missing values.

*State-dependence and repeatability of aggression*

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 aggression tests (218 female, 151 male). In 2018, 56 individuals were assayed (29 females, 27 males), and in 2019, 67 individuals were assayed (35 females, 32 males). There were 16 individuals (11 females, 5 males) that were assayed in both seasons. Analyses of aggression as a function of ‘Sex’, ‘Nest Stage’ and ‘Year’ found no significant difference between female (β = -1.29, 95% CI = -1.45, -1.18) and male (β = -1.22, 95% CI = -1.37, -1.10) aggression, although there was a tendency for males to be more aggressive on average compared to females. We also found strong support that peregrines adjusted levels of aggression across nest stages (Table 1). Aggression was highest during the provisioning stage (β = -0.30, 95% CI = 0.18, 0.41) and lowest during egg laying (Table 1). We found strong support for an effect of ‘Year’ (β = -0.14, 95% CI = -0.13, -0.16) with peregrines decreasing aggression between years with lower aggression levels occurring in 2019 compared to 2018. We found strong support for moderate short-term repeatability (i.e., within-year) (r = 0.37, 95% CI = 0.32, 0.41), and long-term repeatability (i.e., between-year) repeatability (r = 0.19, 95% CI = 0.16, 0.24) of aggression. Long-term repeatability was significantly lower than short-term repeatability (i.e., 95% CI were non-overlapping).

*(Dis-)assortative mating*

We had 148 unique pair-level assays (2018 = 75 assays, 2019 = 73 assays) 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 between-pairs in 2018 (β = 0.34, 95% CI = -0.29, 0.72, Bayesian p-value = 0.17). We found weak support for a positive within-pair correlation (β = 0.14, 95% CI = -0.16, 0.36, Bayesian p-value = 0.24). In contrast, in 2019, we found strong support for disassortative mating between-pairs (β = -0.54, 95% CI = -0.82, -0.02) and strong support for a positive within-pair correlation (β = 0.40, 95% CI = 0.21, 0.63).

*Fitness models*

We analyzed each of the fitness measures described above as a function of ‘Sex’ × ‘Year’ × ‘Aggression’. First, we evaluated the probability to successfully fledge a chick. We used the first test of a given year as an individual’s aggression score for that year, which left us with n = 123 individuals at n = 30 nests in 2018 and n = 34 nests in 2019. We found no support for aggression to influence fitness in either sex in 2018, but we found strong support for higher aggression being associated with a higher probability of fledging at least one chick in both females (β = 2.96, 95% CI = 1.29, 5.00) and males (β = 3.45, 95% CI = 1.03, 5.83) during the 2019 season. Next, we excluded nests that did not fledge at least one chick in order to ask, among-successful nests, whether aggression predicted the number of chicks fledged. These analyses were conducted on n = 37 individuals at n = 14 nests in 2018 and n = 10 individuals at n = 5 nests in 2019. Since we only had two repeated measures, we did not have enough power to include ‘ID’ as a random effect but instead we included ‘SiteID.’ We found strong support that higher aggression was associated with fledging fewer chicks in both females (β = -0.60, 95% CI = -0.95, -0.28) and males (β = -0.63, 95% CI = -0.89, -0.28) in 2018. The opposite was true in 2019. In 2019, there was strong support that higher aggression in males was associated with fledging more chicks (β = 0.47, 95% CI = 0.02, 0.74), and moderate support for the same effect in females (β = 0.18, 95% CI = -0.09, 0.53). Lastly, we assessed if aggression predicted chick mass at fledging. A total of n = 27 chicks fledged during the 2018 season at n = 14 nests, and n = 7 chicks fledged during the 2019 season at n = 5 nests. Analysis of chick mass at fledging found strong support that higher aggression was associated with lower mass at fledging in both females (β = -14.80 , 95% CI = -25.62, -5.09) and males (β = -13.91, 95% CI = -23.42, -4.75) during the 2018 season. In contrast, we found strong support for higher aggression being associated with greater mass at fledging for both females (β = 11.25, 95% CI = 3.09, 20.10) and males (β = 15.45, 95% CI = 5.94, 27.00) in 2019.

**DISCUSSION**

In this study, 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 across years. In 2018, there was moderate support for assortative mating by aggression score, and higher aggression in both males and females was associated with lower reproductive success. In contrast, in 2019, there was weak evidence of disassortative, but for both males and females, higher aggression 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 aggressive and non-aggressive 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 more aggressive than males (Wiklund and Stigh, 1983; Andersson and Wiklund, 1987; Wiklund, 1990a). Surprisingly, in our population males tended to dive closer on average than females (Male mean = 25m, Female mean = 28m), though this difference was not significant (Table 1). Our finding of relatively similar aggression scores in males and females is in contrast to studies in other raptors that found higher investment by females (Long-eared owl, Galeotti et al., 2000; Ural owl, Kontiainen et al., 2009; Northern Goshawk, Møller and Nielsen, 2014; Montagus harrier, Arroyo et al., 2017). We suggest that the similar levels of aggression observed in male and female Peregrines in our study may be due to environmental constraints. Since conditions are often unforgiving in the Arctic (i.e., snowstorms during egg laying and incubation, high winds, low temperatures, high density of biting bugs, exposed nest sites) high investment into incubation and brooding by females may preclude them from also investing heavily in nest defense, resulting in relatively similar investment in nest defense across the sexes in our study. This may imply that the degree of difference between males and females may depend on year-specific environmental conditions, with females being more aggressive than males in years with relatively benign conditions, though this suggestion requires further study.

We also found that nest defense increased (i.e., individuals dove closer to observer on average) as a function of nest stage with the most aggressive responses occurring during the provisioning stage and the least aggressive responses 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. Peregrines breeding in Rankin Inlet have a narrow range of laying dates (~12 days; Bradley et al., 1997), in order to successfully produce chicks 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 aggression over the nesting stage likely reflects the increased chance of fledging a chick while simultaneously reflecting the low prospective for re-nesting. Similar patterns of increasing nest defense with advancing nest stage has been observed in numerous other studies in 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 chicks 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 species of birds (Both et al., 2005; Schuett et al., 2011; Gabriel and Black, 2012; Burtka and Grindstaff, 2015). Unexpectedly, we found evidence for assortative mating in one year of the study (2018) and disassortative mating in the second year of the study (2019). Pairs that mated assortatively and were the most aggressive had lower reproductive success in 2018, and the opposite for 2019 with higher reproductive success associated with pairs that had an aggressive male or female. Similarly, Both et al. (2005) found evidence for both assortative and disassortative mating by exploratory behavior in the same great tit population within a 3-year period with the direction of the fitness benefit fluctuating temporally with the behavioral type that was favored in each environment. We hypothesize that mate choice in peregrine falcons is likely context dependent in which the environmental conditions regulate how behavioral types are valued (Munson et al., 2020). In this scenario, 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 or access to a high-quality territory. In poor years when food availability is low females could be selecting for direct benefits that are related to food acquisition. For example, females could use aggression as a cue for their partners 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 male aggression. Likewise, aggression could be an honest cue of the quality and size of the territory a male possesses which would be beneficial in years with low resources. Further study is needed to understand how male aggression covaries with provisioning ability in order to determine if there are any direct benefits of mate choice. However, the fact that breeding adults mated assortatively in one year, and disassortatively in the other, reveals that the stable among-individual differences in aggression observed in this study cannot be explained by shared stable environmental differences among-pairs (e.g., territory quality), and are at least partially due to among-individual differences in state.

Finally, we explored the consequences of among-individual differences in nest defense for reproductive success. We found aggression to influence reproductive success, but the direction of the relationship varied between years. In one year of the study (2018) more aggressive individuals were less likely to fledge any chicks, and if they did fledge chicks, they fledged fewer chicks and these chicks fledged at lower body mass. In 2019, the opposite was true. More aggressive individuals were more likely to fledge chicks, fledged more chicks and fledged chicks at higher body mass. In both years, the patterns were the same for both males and females, indicating that selection acted on male and female aggression in the same way within-years, though in one year (2018) lower aggression was favored and in the other year (2019) higher aggression was favored. This adds 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 could 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, density fluctuations could also be associated with our findings of fluctuating selection. Although, we only have two years to compare, we observed fluctuations in breeding densities between years (2018 n = 28 breeding pairs, 2019 n = 34 breeding pairs) with aggressive behavioral types doing better in high density years and non-aggressive behavioral types doing better in lower density years. We could attribute this to 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 aggression and provisioning (e.g., Betini and Norris, 2012). For example, if more aggressive individuals are more responsive to variation in offspring need as has been shown in other species (Betini and Norris, 2012), they may outperform less aggressive individuals when weather conditions are more challenging. Year-specific weather conditions are consistent with this idea. Weather conditions obtained from Environment Canada (2021) website, in Rankin Inlet during July and August (i.e., critical hatching and chick rearing phases) was markedly different from 2018 to 2019. During the 2018 season Rankin Inlet received fewer heavy rain events (i.e., precipitation events ≥ 8 mm/day; Bradley et al., 1997), 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). Individuals that were more aggressive during the 2019 season had higher reproductive success and produced chicks with higher average mass during a year with more heavy rain events and total precipitation as compared to 2018. Future work should evaluate the proposed relationship between nest aggression and provisioning.

*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 (e.g., territory quality), because we only observed apparent assortative mating in one year, while in the other, there was weak evidence for disassortative mating. However, we also found strong support for fluctuating selection acting on behavioral types. We suggest that aggression may be valued in years with high inter-specific competition and/or high 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 trade-offs with other parental care behaviors such as provisioning behavior, and whether this provides a mechanism for the fluctuating selection documented here.

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

|  |  |
| --- | --- |
|  | **Aggression 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) |  |
| Residual | 0.14 (0.13, 0.16) |
| Individual | 0.04 (0.03, 0.06) |
| Individual Series | 0.04 (0.03, 0.05) |
| **Repeatability**  r (95%CI) |  |
| Short-term repeatability | 0.37 (0.32, 0.41) |
| Long-term repeatability | 0.19 (0.16, 0.24) |

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
|  | **Measures of fitness** | | | |
| **Probability of fledging a chick** | **Number fledged** | **Chick mass at fledging** |
| **Fixed effects** β (95% CI) |  |  |  |
| Sex × Year × Aggression |  |  |  |
| Female × 2018 × Aggression | 0.32 (-1.11, 1.39) | **-0.60 (-0.95, -0.28)** | **-14.80 (-25.62, -5.09)** |
| Male × 2018 × Aggression | 0.35 (-1.12, 1.55) | **-0.63 (-0.89, -0.28)** | **-13.91 (-23.42, -4.75)** |
| Female × 2019 × Aggression | **2.96 (1.29, 5.00)** | 0.18 (-0.09, 0.53) | **11.25 (3.09, 20.10)** |
| Male × 2019 × Aggression | **3.45 (1.03, 5.83)** | **0.47 (0.02, 0.74)** | **15.45 (5.94, 27.00)** |
| **Random Effects**  σ (95% CI) |  |  |  |
| Residual | 1 | 0.09 (0.06, 0.15) | 63.07 (38.47, 102.12) |
| Site ID | 22.14 (14.75, 32.27) | 0.74 (0.53, 1.03) | 9238.61 (8389.91, 10101.79) |
| Individual | 0.00 (0.00, 0.00) |  |  |

**Table 2.** Results from models assessing probability of fledging a chick, number of chicks fledged, and chick mass at fledging. The effect size estimates (β), and their 95% credible intervals (CI) are reported. Significant fixed effects are in bold.

**Figure 1.** 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 aggression and negative ‘Minimum Distance’ values are equated to low aggression. 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.

![Chart, scatter chart

Description automatically generated]()

**Electronic Supplementary Material**

**ESM Table S1.** Results from PCA on measures of nest defense. Significant loadings and eigenvalues are in bold.

|  |  |  |  |
| --- | --- | --- | --- |
| **Measures of nest defense**  **(loadings)** | **PC1** | **PC2** | **PC3** |
| FID | 0.35 | -0.88 | -0.29 |
| Dives | **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 |

**ESM Figure S1.** Results from PCA of nest defense measures. Minimum distance and dive correlated as expected with peregrines that dove more often also dove closer to the observer.

Chart, scatter chart

Description automatically generated