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ARTICLE

Nest defense and parental investment in Song Sparrows (*Melospiza melodia*)N. Morrell ¹, K. M. Johnson ², C. E. Tarwater ³, and P. Arcese ⁴

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1 Nest defense and parental investment in Song Sparrows (*Melospiza melodia*)

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3
4 ABSTRACT.--- Individual variation in nest defense behaviour is common in altricial birds, but
5 despite clear predictions about why such variation exists there is no consensus on its causes. We
6 tested for an influence of five predictors of individual variation in nest defense behaviour,
7 including time of season, offspring age, parental age and sex, and clutch size in a well-studied
8 Song Sparrow (*Melospiza melodia* (Wilson, 1810)) population. We recorded parental responses
9 to a standardized human approach and used model selection to assess support for each predictor.
10 Parents tended to approach observers less closely and alarm-call less as the breeding season
11 progressed, indicating a modest seasonal decline in parental nest defense, consistent with the
12 hypothesis that the reproductive value of offspring influenced parental defense behaviour. Clutch
13 size effect estimates were insignificant, but it was weakly supported as a predictor of nest
14 defense, as expected if parental investment in defense and current reproductive effort are
15 positively related. Offspring age, and parental age and sex received little or no support as
16 affecting parent nest defense. Our results offer limited support for the hypothesis that the
17 reproductive value of offspring affects parental nest defense.

18 Key words: nest defense, breeding phenology, altricial birds, life history, *Melospiza melodia*,
19 Song Sparrow

Parental investment in nest defense has been extensively studied in birds, but without reaching consensus on the mechanisms driving it. Nest defense is thought to involve trade-offs by reducing the rate of depredation but increasing the risk of injury or death to parents (Montgomerie and Weatherhead 1988). Variation in nest defence has thus been linked to a number of life-history traits including parental age (Ricklefs 1977; Smith et al. 1984), sex (Weatherhead 1989; Winkler 1992; Trnka and Prokop 2010; Polak 2013), offspring age (Ricklefs 1969; Andersson et al. 1980; Patterson et al. 1980; Curio et al. 1984; Pavel 2006), clutch size (Curio and Regelmann 1987; Wiklund 1990; Kazama et al. 2010; Svaglieij et al. 2011), time of breeding season (Curio et al. 1984; Wallin 1987; Weatherhead 1989; Redmond et al. 2009; Boukhriss and Selmi 2010; Klvaňová et al. 2011), nest concealment (Maclean et al. 1986; Eggers et al. 2008), and the characteristics of predators (Hatch 1997; Hogstad 2004). We focus here on the influence of time of season, offspring age, parental age and sex, and clutch size on parental nest defense behaviour in a well-studied population of Song Sparrows (*Melospiza melodia* (Wilson, 1810)), where we were able to control for many potentially confounding effects. We now review existing theory and empirical results to identify specific predictions.

Life history theory links breeding phenology and residual reproductive value to parental investment, but empirical evidence remains scarce (Caro 2005). For example, as the breeding season progresses and opportunity to re-nest declines, nest defense is predicted to increase (Montgomerie and Weatherhead 1988). Similarly, older birds are predicted to respond more strongly to threats at the nest than younger birds if re-nesting potential declines with parental age (Pianka and Parker 1975; Boukhriss and Selmi 2010). In contrast, theory and some empirical results suggest that nest defense declines as breeding progresses because offspring that fledge later often have lower survival and thus have lower residual reproductive value and receive less

parental investment (Curio et al. 1984; Wallin 1987; Weatherhead 1989; Redmond et al. 2009; Klvaňová et al. 2011; Svagelj et al. 2011). However, only a few studies report precise estimates of parental age, and those that do typically report no link between parental age and nest defense (Weatherhead 1989; Winkler 1992; Hatch 1997). Moreover, although Smith et al. (1984) showed that older parents responded more strongly to Brown-headed cowbirds (*Molothrus ater*) at the nest, a key nest predator (Arcese et al. 1996), their results were positively related to parental experience with cowbirds but not residual reproductive value.

In polygamous species, the sex of a parent often predicts nest defense behaviour and is typically higher in the sex most closely related to nestlings on average (Montgomerie and Weatherhead 1988; Trnka and Prokop 2010). In contrast, in monogamous species defense mainly varies with traits of the pair rather than between the sexes (Regelmann and Curio 1983; Weatherhead 1989). The Song Sparrows we studied exhibit social monogamy but genetic polygyny (Sardell et al. 2010), making predictions less clear. If males adjust parental care by certainty of paternity, they should engage less in nest defense than females, unless doing so further reduces their success as a sire.

Clutch size and offspring age may also affect parental nest defense (Andersson et al. 1980; Patterson et al. 1980; Pavel 2006; Svagelj et al. 2011). Defense is predicted to increase with clutch size given a commensurate increase in reproductive value. Similarly, defense is predicted to increase with offspring age because the probability offspring survive to recruitment increases with age. Correspondingly, several studies report positive links between clutch size, offspring age, and parental nest defense (Curio et al. 1984; Caro 2005; but see Montgomerie and Weatherhead 1988).

Our goal was to test if time of season, nest age, parental age or sex, or clutch size predicted parental nest defense in an individually-marked population of Song Sparrows wherein each of the factors above was known with precision. Specifically, we tested for the effect of season, parent age and sex, offspring age and clutch size on parental nest defense behaviour in response to standardized human approach and then ranked the relative importance of these factors using multi-model inference. Based on a long history of study in this population, we predicted that: a) parental nest defense would decline as the season progressed; b) older parents would respond more strongly to threats at the nest than younger parents; c) females would engage in more vigorous nest defense than males; and d) nest defense would increase with clutch size and e) offspring age.

METHODS

Study System.---We studied a resident Song Sparrow population on Mandarte Island (*c* 6 ha), British Columbia, from April to July 2014, where 99% of breeding birds are individually marked as nestlings and have been monitored in detail from 1975 to present. Females build open-cup nests, typically low in shrub, grass, and herbaceous vegetation and lay 2–4 eggs, 1–4 times per season. Breeding pairs occupy territories 200–5000 m², and are socially monogamous but genetically polygamous (details in Smith et al. 2006). All birds in our study were color-banded as nestlings and monitored every 3–5 d from April through July to identify territory boundaries, social mates, and locate all nests, mainly during nest-building or early incubation. Once found, nests were monitored every *c* 5 d to check for hatching or to band nestlings (*c* 6 d old; Smith et al. 2006). Confirmed nest predators of song sparrow nests on Mandarte Island include brown-headed cowbirds, deer mice, northwestern crows, red-winged blackbirds, European starlings, Glaucous-winged gulls, and river otters (Arcese et al. 1996; Smith et al. 2006). During nest

visits, song sparrows react to humans with the same suite of behaviours and with similar intensities to those opposed in experimental trials with predator models (Smith et al. 1984). The study was conducted in a low density year where territories were uniformly large and neighboring pairs were not seen to interfere with individual response.

Field Protocol.--- We quantified nest defense behaviour during incubation and at banding using a standardized human approach. A trial commenced when an observer was 15 m from a focal nest by noting the presence of one or both parents as “on” or “away from nest”. As observers slowly approached the nest, a recorder noted the closest approach of each parent to the observer and the type of vocalization as “chips”, “tchunks”, or “none”, in order of decreasing intensity (Nice 1964). Parents that did not respond to a trial by remaining out of sight were assigned a closest approach of 40 m, which was beyond the distance at which responding birds were recorded. We explored the consequences of using 40 m and found that the distance assigned did not influence the results. At banding, we recorded parental behaviour upon first approaching the nest and when returning banded chicks to the nest. In all cases, we recorded latency time of the first parent to return to the nest with the observer positioned at a static distance of 15 m from the nest. Temperature, cloud cover, wind speed (“high” or “low”) and time of day were also recorded at each trial. We monitored 47 individuals and 24 breeding pairs. Two to six trials were conducted per breeding pair throughout the breeding season, with an average of four trials per pair, to a total of 179 trials across individuals.

Data Analysis.--- All analyses were conducted in R 3.1.2 (R Core Development Team 2014) to estimate relationships between response variables (closest approach, vocalizations, latency to return to nest) and a suite of predictor variables in a mixed effects modelling framework. Parent age and clutch size were treated as integers, and we assigned an age of four to

two individuals ($n=8$) that were older than four years to account for small sample size. Closest approach and latency were modeled as the proportion of each trial to the maximum overall value recorded, using generalized linear mixed models assuming a beta distribution and logit link. A beta distribution minimized residual variance as compared to Poisson or Gaussian distributions. Vocalization type was analysed using a multinomial mixed effects model, Poisson distribution and logit link. We used the glmmADMB package (Fournier et al. 2012; Skaug et al. 2013) and nnet package (Venables and Ripley 2002) to fit beta-distributed and multinomial models, respectively, and the MuMIn package (Bartoń 2016) for model selection.

We selected Julian date to represent time of season but excluded nest attempt because it was closely correlated with Julian date (Spearman's rank $|>0.7|$). Trial length was included as a covariate in the global model to account for the possibility that longer trials were more likely to elicit responses. Initial analyses suggested wind speed and initial proximity also predicted parental behaviour (see also Ibarra et al. 2014; Lord et al. 2001); thus we included these factors as covariates in the global model. Clutch size, Julian date, offspring age, parental age and sex were treated as fixed effects. The individual identity of the bird was included as a random-effect. We created a model for each combination of predictors, then ranked models using Akaike's Information Criteria corrected for small sample sizes (AIC_c), where smaller AIC_c indicated better model fit (Burnham and Anderson 2004). Models with a $\Delta AIC_c \leq 2$ from the best-fitting model were considered supported, and models with ΔAIC_c from 2-4 were considered to have limited support (Burnham and Anderson 2004). Effect sizes and standard errors were averaged by model weight and parameter estimates reported for models with $\Delta AIC_c \leq 4$.

RESULTS

One or both parents responded to observers in 65% of 179 trials and approached to within two meters of observers in 19% of trials. The best model of closest approach included Julian date, followed by Julian date and offspring age, and Julian date and clutch size ($w_i = 0.039$, 0.030, and 0.027 respectively; Table 1). Julian date was included in 14 of 16 top models ($\Delta AIC_c \leq 2$), and models with Julian date had a cumulative weight of 0.67, indicating that time of season was a more consistent predictor of closest approach than parent age, clutch size, offspring age or sex. Clutch size and offspring age were included in 7 and 6 top models, and were included in models with a cumulative weight of 0.47 and 0.42, respectively. Parent sex and parent age were each included in only one top model ($\Delta AIC_c = 1.93$ and $\Delta AIC_c = 1.96$; Table 1). A null model with only random effects included had 26 times less support (evidence ratio of Akaike weights, w_i) than our top AIC_c model ($\Delta AIC_c = 6.52$), indicating that all predictors, but particularly Julian date, clutch size, and offspring age, were informative of closest approach to the observer.

In contrast, model-averaged effect sizes for predictors of interest in our closest approach models where $\Delta AIC_c \leq 4$ all had 95% confidence intervals that included 0. Nevertheless, parents tended to approach observers less closely as the season progressed (0.012 ± 0.006 ; Table 2) and more closely as clutch size increased (-0.179 ± 0.132 ; Table 2), but these trends were not statistically significant. Parents initially on the nest were significantly more likely to approach the observer closely (-1.188 ± 0.469 ; Table 2).

Latency to return to nests was only recorded in 26% of trials, because nest concealment prevented precise estimates in most cases. No model of latency returned an AIC_c value less than the null model; hence we excluded latency from further analysis.

One or both parents exhibited tchunks in 46% of trials and chipped in 11% of trials. The only model of vocalization type with substantial support ($\Delta AIC_c \leq 2$) included Julian date

(Akaike weight, $w_i = 0.34$; Table 3). Models with Julian date had a cumulative weight of 0.96. There was limited support for a model with Julian date and clutch size ($\Delta AIC_c = 2.21$; Table 3) and a model with Julian date and age ($\Delta AIC_c = 2.59$; Table 3). A null model with only random effects included had 272 times less support (evidence ratio of Akaike weights, w_i) than our top AIC_c model ($\Delta AIC_c = 11.21$), indicating that all predictors, but particularly time of season, were informative of vocalization.

With the exception of a negative relationship between Julian date and tchunks, model-averaged effect sizes for predictors of interest in vocalization models where $\Delta AIC_c \leq 4$ all had 95% confidence intervals that included 0. Parents were significantly less likely to tchunk as the season progressed (-0.029 ± 0.010 ; Table 4), and significantly more likely to tchunk in high wind conditions (1.540 ± 0.532 ; Table 4).

DISCUSSION

Parental song sparrows tended to approach human observers at their nest more closely and were more likely to vocalize early in the season, consistent with the hypothesis that adults reduce investments in the defense of young that are themselves less likely to become breeders. In seasonal environments, timing of breeding is often linked to breeding success (e.g., Serra et al. 2012) and in altricial birds, later nesting attempts typically produce young that survive less well (Crick et al. 1993; Gruebler and Naef-Daenzer 2008), including among song sparrows on Mandarte Island (Hochachka and Smith 1991). We also noted that parents that bred late in the season tended to be those exhibiting high fledging success earlier in the year, consistent with the idea that later broods were less valuable. Seasonal declines in response to threats at the nest are often attributed to declines in offspring quality, parent quality or both (Weatherhead 1989;

178 Redmond et al. 2009; Klvaňová et al. 2011; Svagelj et al. 2011; but see Pavel 2006; Boukhriss
179 and Selmi 2010).

180 To address the possibility that individuals became habituated to repeat visits to nests by
181 human observers, we tested for an interaction between the number of times an individual had
182 been visited at the nest in its lifetime with the seasonal trend in defense. If the seasonal decline in
183 response were due to habituation, we would expect individuals with many lifetime visits to show
184 a decreased response. We found no support for an interaction, and instead found that individuals
185 with more encounters with humans tended to respond more strongly, consistent with Knight and
186 Temple (1986).

187 We found weak support for an effect of clutch size on nest defense, but almost no
188 evidence that parental age or sex affected nest defense. Nests with larger clutches tended to elicit
189 closer approaches, consistent with the hypothesis that parental nest defense should increase with
190 reproductive value of nest contents (Montgomerie and Weatherhead 1988; see also Curio and
191 Regelman 1987; Wiklund 1990; Kozma and Kroll 2010; Svagelj et al. 2011). Interestingly,
192 studies failing to support this hypothesis tend to focus on longer-lived species with high re-
193 nesting potential (e.g., Kazama et al. 2010). Kozma and Kroll (2010) suggested that positive
194 correlations between nest defense and clutch size might arise via parental quality, with larger,
195 older birds expressing higher reproductive success and nest defense. In contrast, we found no
196 evidence that parental age or sex of parents affected nest defense in a Song Sparrow population
197 in which most individuals breed for one season (Smith et al. 2006).

198 Offspring age was often included in our supported models, but received equivocal
199 support as a predictor of nest defense. Montgomerie and Weatherhead's (1988) prediction that
200 the reproductive value of offspring and parental nest defense will both increase with offspring

age been supported repeatedly (e.g., Andersson et al. 1980; Patterson et al. 1980; Curio et al. 1984; Pavel 2006). In contrast, we found little evidence that parental defense increased with offspring age. Overall, our results show that despite being able to precisely estimate many factors thought to affect parental nest defense, most of the variation in parental response that we recorded remained unexplained; an outcome common to many similar studies. Because consistent individual differences in parental response to threats at the nest have the potential to complicate tests of the hypotheses explored here (e.g., Burtka and Grindstaff 2013) we suggest that researchers revisit individuals repeatedly over multiple seasons to increase sample sizes and refine estimates of individual variation in behaviour.

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TABLE 1. Model selection for general linear mixed-effects models to explain closest approach to observer. Predictors included are indicated by (+) or (-) depending on the direction of effect. K is the number of parameters in the model. ΔAIC_c equals the difference in AIC_c between the best and each successive model, where AIC_c is the Akaike information criterion corrected for small sample size. w_i is the Akaike weight, representing the probability that a model is the best in the model set. ($n=167$).

Model Rank	Par-ent Age	Clutch Size	Julian Date	Off-spring Age	Sex	Trial Length	Initial Behaviour	Wind	K	ΔAIC_c	w_i
1			(+)				(-)		4	0.00	0.039
2			(+)				(-)	(-)	5	0.36	0.033
3			(+)	(+)			(-)		5	0.52	0.030
4		(-)	(+)			(-)	(-)		5	0.79	0.027
5			(+)			(-)	(-)		5	0.93	0.025
6			(+)	(+)			(-)	(-)	6	1.10	0.023
7		(-)				(-)	(-)		6	1.11	0.023
8		(-)	(+)			(-)	(-)		6	1.19	0.022
9		(-)	(+)	(+)			(-)		6	1.28	0.021
10			(+)	(+)		(-)	(-)		6	1.53	0.018
11		(-)	(+)				(-)	(-)	6	1.58	0.018
12			(+)			(-)	(-)	(-)	6	1.74	0.017
13		(-)		(+)		(-)	(-)		6	1.76	0.016
14		(-)	(+)	(+)		(-)	(-)		7	1.77	0.016
15			(+)		(-)		(-)		5	1.93	0.015
16	(-)		(+)				(-)		5	1.96	0.015
NULL									2	0.00	0.039

TABLE 2. Averaged, logit-scale effect size estimates, standard error, standard error adjusted for heteroscedasticity, and 95% confidence intervals for variables predicting closest approach to observer. Effect sizes indicate the number of units of change in the predictor variable for a one unit increase in the response. Coefficients are averaged by model weight across models within $\Delta AIC_c < 4$ of best model and use restricted maximum likelihood estimates ($n=167$).

Predictor	Estimate	Standard Error	Adjusted SE	Lower CI	Upper CI
(Intercept)	-0.939	1.605	1.610	-4.095	2.218
Parent Age	-0.018	0.108	0.109	-0.231	0.196
Clutch Size	-0.179	0.132	0.133	-0.439	0.081
Julian Date	0.012	0.006	0.006	0.000	0.024
Offspring Age	0.059	0.047	0.048	-0.035	0.152
Sex (male)	-0.091	0.212	0.213	-0.509	0.328
Trial Length	-0.046	0.036	0.036	-0.117	0.025
Initial Behaviour (on nest)	-1.188	0.469	0.472	-2.114	-0.262
Wind (low)	-0.305	0.271	0.273	-0.839	0.229

TABLE 3. Model selection for multinomial mixed-effects models optimized for vocalization type. Conventions follow Table 1 ($n=179$).

Model Rank	Parent Age	Clutch Size	Off-spring Age	Julian Date	Sex	Trial Length	Initial Behaviour	Wind	K	ΔAIC_c	w_i
1				(-)				(+)	4	0.00	0.342
2		(+/-)		(-)				(+)	5	2.21	0.113
3	(+/-)			(-)				(+)	5	2.59	0.094
4				(-)			(+)	(+)	5	3.89	0.049
NULL									2	11.21	0.001

331 TABLE 4. Average logit-scale effect size estimates, standard errors, and 95% confidence
 332 intervals for variables predicting vocalization type in multinomial models. Conventions follow
 333 Table 2 ($n=179$).

Response	Predictor	Estimate	Standard Error	Lower CI	Upper CI
Tchunk vs. none	(Intercept)	2.883	1.622	-0.296	6.062
	Parent Age	-0.134	0.174	-0.475	0.207
	Clutch Size	-0.032	0.199	-0.421	0.358
	Julian Date	-0.029	0.010	-0.049	-0.010
	Initial Behaviour (on nest)	0.187	0.785	-1.352	1.725
	Wind (low)	1.540	0.532	0.497	2.583
Chip vs. none	(Intercept)	-3.015	2.573	-8.057	2.027
	Parent Age	0.209	0.244	-0.270	0.687
	Clutch Size	0.446	0.340	-0.219	1.112
	Julian Date	0.006	0.015	-0.023	0.035
	Initial Behaviour (on nest)	0.632	0.893	-1.119	2.383
	Wind (low)	0.254	0.626	-0.973	1.482

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