1 **Evolved parental responses to offspring solicitation reflect energetic demands,**

2 **environmental predictability, and offspring predation risk**

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26 **Abstract:**

27 Parental responses to offspring solicitation differ among species and have major implications for

28 fitness, but the evolutionary drivers of this diversity are poorly studied. Here, we experimentally

29 amplified begging calls at nests of 25 songbird species in tropical and north temperate

30 communities. We analyzed parental provisioning responses using phylogenetic path analysis to

31 test the possible roles of demographic (offspring predation or adult survival rates), ecological

32 (food predictability) or physiological (offspring energy need) traits in the evolution of parental

33 responsiveness to begging. Species with smaller body mass, more unpredictable food

34 availability, and greater offspring predation rates were more responsive to begging. In contrast,

35 we found little support for direct effects of adult survival on parental responses. Ultimately, the

36 evolution of parental responsiveness to offspring solicitation is strongly related to energetic

37 needs of young and the predation costs of begging.

38

Introduction:

Parents must balance the effort of caring for their young to increase current reproductive success against self-maintenance to increase future reproductive success (Williams 1966; Charlesworth 1994; Roff 2002). Across taxa, offspring often provide signals to parents about their energetic need for care that may help parents make decisions to achieve this balance (Godfray 1991; Godfray 1995; invertebrates: Smiseth & Moore 2002, amphibians: Yoshioka et al. 2016, mammals: Manser & Avey 2000, birds: Clark & Lee 1998). However, parental provisioning responses to variation in offspring begging vary widely among species (Clark & Lee 1998; Price 1998; Grodsinski & Lotem 2007; Tarwater et al. 2009; Haff & MacGrath 2011). In some species, parents provisioned broods substantially more with increased begging cues, but, in other species, begging intensity had little or no impact on parental provisioning. Given the ubiquity of offspring solicitation across taxa, understanding why species differ in parental responses to these signals is critical for determining the evolutionary bases of parental effort and parent-offspring communication.

Previous theory and empirical work within single species highlight numerous possible causes of variation in parental responsiveness to begging. One possibility is that parental responsiveness to offspring begging varies with longevity and the probability of future reproduction. In shorter-lived species, parental fitness is closely tied to the survival of current young (Williams 1966; Charlesworth 1994, Ghalambor and Martin 2001, Roff 2002), so parents may respond to offspring begging by increasing provisioning (Kilner & Hinde 2008). In contrast, future offspring provide a greater share of lifetime fitness in parents of longer-lived species (i.e. higher survival rate and greater residual reproductive value; Williams 1966; Charlesworth 1994, Roff 2002). Parents of long-lived species, therefore, may not increase provisioning in response to

62   offspring begging in order to minimize costs of reproduction, enhance self-maintenance, and

63   increase chances of reproducing in the future (Kilner & Hinde 2008). Thus, the evolution of

64   parental responsiveness to offspring begging may be shaped by variation in adult survival among

65   species (*future reproduction hypothesis*). Provisioning rates differ among species related to adult

66   survival rates (Martin 2015), but whether responsiveness to offspring begging varies with adult

67   survival rates is unknown.

68   Offspring predation risk may also influence parental responsiveness to begging in at least

69   two ways. First, parental provisioning activity can help predators locate young (Skutch 1949;

70   Martin et al. 2000; Muchai and DuPleiss 2005), and parents may mitigate predation risk by

71   providing care based on perceived safety rather than offspring begging cues. Consequently,

72   species with greater offspring predation rates may have evolved lower responsiveness to begging

73   than species that experience little offspring predation (*predation constraint hypothesis*). Second,

74   offspring may have evolved to leverage the fact that begging cues can attract predators as a way

75   to "blackmail" parents to provide more care (*blackmail hypothesis*; Zahavi 1977; Haff &

76   MacGrath 2011; Thompson et al. 2013). This strategy should be more effective in species with

77   greater offspring predation rates. Consequently, parents of these species may evolve greater

78   responsiveness to begging than species with lower predation rates, opposite to the *predation*

79   *constraint hypothesis*.

80   A third hypothesis centers on the energetic needs of offspring and parental time

81   efficiency for providing care (*energetic requirements hypothesis*; Grodsinski & Lotem 2007).

82   The time from when offspring first begin to beg and begin to suffer fitness costs may be

83   relatively short when offspring have high energetic expenditure due to high mass-specific

84   metabolism and low capacity to store energy (e.g., species with small body mass). In this case,

4

85   parents will be able to provide care when it is needed the most by responding promptly to

86   offspring begging. In contrast, offspring with lower mass-specific metabolic rate and greater

87   ability to store energy (e.g., large body mass) may be able to beg for a much longer time before

88   lack of care yields costs. If energy requirements of offspring are important, parents should be

89   less responsive in larger than smaller species (Grodsinski & Lotem 2007).

90   Finally, the predictability of food resources may influence the evolution of parental

91   responsiveness to begging (Caro et al. 2016). A meta-analysis showed that bird species with

92   greater levels of brood reduction from poor and unpredictable environmental conditions

93   preferentially fed offspring in better condition rather than nest mates that begged most intensely

94   (i.e. unresponsive to begging; Caro et al. 2016). Species that feed siblings based on structural

95   cues about condition instead of responding to begging may maximize their chance of at least one

96   offspring surviving even if the odds that some young will die (i.e., brood attrition) also increase

97   (Grafen 1990; Mock et al. 2011). While these ideas have been examined in the context of

98   allocating food among nestmates, they may also apply to differences in parental responsiveness

99   to begging across broods. Species that experience unpredictable food supply should have lower

100   reproductive value for any given brood because food supplies could deteriorate (Martin 1987).

101   Thus, species that experience more unpredictable food availability may be less responsive to the

102   overall intensity of begging from all young in the nest than species with more constant food

103   availability (*environmental predictability hypothesis*). Alternatively, parental responsiveness in

104   species facing unpredictable food supply may depend on the current conditions. In this case, such

105   species may be highly responsive to begging as long as food is abundant, but become less

106   responsive only when environmental conditions become poor. Ultimately, the idea that species

107 that differ in predictability of food supply (e.g. as reflected by average brood attrition) adjust

108 total provisioning based on offspring solicitation cues is untested.

109   Here we conducted a standardized playback experiment to increase the intensity of

110 begging cues at nests in 25 species of tropical and north temperate songbirds and examined

111 parental responses in feeding activity (Table S1; Fig. S1). We compared parental responsiveness

112 across species differing in adult survival, nest predation rates, nestling body mass, and brood

113 attrition rates and used phylogenetic path analysis to test the relative importance of alternative

114 hypotheses.

115

116 **Methods:**

117 *Data collection:*

118   We studied 18 songbird species in primary tropical montane forest at Kinabalu Park in

119 Sabah, Malaysia from 2009-2019, and 7 species from mixed temperate forest in central Arizona,

120 USA from 1987-2017. We found and monitored nests between February and June in Malaysia

121 and April through July in Arizona. We recorded brood size and survival of young from hatching

122 until fledge to determine nest predation rates. We calculated brood attrition rates as the

123 percentage of nests where at least one young died prior to fledging. As a measure of offspring

124 size, we also weighed nestlings on the day when the primary flight feathers begin to break out of

125 their sheaths (hereafter pin break) to control for developmental stages across species.

126   We used standard effort mist netting along with resighting of color-banded birds to

127 estimate annual apparent adult survival based on Cormack-Jolly-Seber models (Martin et al.

128 2015, 2017). At both sites, we used 12 nets at each netting plot and sampled each plot 3 times

129 over the course of the breeding season. We opened nets for 6 hours each day beginning at

130   sunrise. Birds were marked with aluminum bands with unique identifiers and three plastic color

131   bands in a unique arrangement to facilitate identifying individuals through resighting. Birds were

132   resighted opportunistically throughout each study area by nest searchers.

133   Begging calls for each species were recorded on pin break in the field using a digital

134   recorder (PMD 661 by Marantz, Chatsworth, CA, USA) and small lapel microphone (model

135   AT831C; Audio-Technica, Tokyo, Japan). The microphone was placed exactly 15 cm away from

136   the inside edge of the nest cup. We ensured all settings (e.g. gain) were identical on the recorder

137   for each recording. All recordings were made on nests with typical brood sizes for each species

138   and at a standardized developmental stage (pin break) to allow comparisons across species.

139

140   *Playback Experiment:*

141   We conducted begging playback experiments in 2016-2018 in Malaysia and 2016-2017

142   in Arizona. Within 1-2 days of pin break, we placed small camouflaged speakers (Groove Cube

143   by WowWee Group Limited, Hong Kong) immediately adjacent to nests and set up a video

144   camera to film parental behavior. We first filmed nests for at least 80 mins without the speakers

145   broadcasting anything to allow parents to acclimatize to the presence of the speakers. Then we

146   played either begging call recordings from the same species or white noise as a control for 80

147   mins. We constructed playback recordings with 10 seconds of sound (either begging or white

148   noise) followed by 50 secs of silence each minute to simulate bouts of begging. Each playback

149   recording consisted of begging recordings from at least 4 unique nests for each species. We

150   alternated whether we played the begging recordings or control recordings first for each nest in a

151   species. After 80 mins the recording automatically switched treatments (i.e. the control began

152   playing if the begging recording was played first). All recordings were played at typical volumes

153   for each species as measured by a sound level meter at 15 cm from nestlings without obstructions

154   (Model 407730, Extech Instruments Corporation). The average volume of control and begging

155   recordings were similar. All playback experiments began at about the same time each day (0730-

156   0930). We conducted playback experiments at an average of 7 nests per species (Table S1).

157

158   *Statistical Analyses:*

159   Nest predation rates during the nestling period were estimated using the logistic exposure

160   method (Shaffer 2004). We included species as a fixed effect and included nested random

161   intercepts for year within site.

162   To obtain a measure of parental responsiveness to experimental begging playback for

163   each species, we used a hierarchical Bayesian model. We modeled the number of feeding trips

164   during each 80min treatment period using a Poisson distribution and a log link function. For each

165   species, we included brood size and developmental state (days relative to pin break) as covariates

166   and a fixed effect for the experimental treatment (begging or control; β_{beg}). We also included a

167   random intercept to account for nest ID, an offset to account for slight variation in the length of

168   playback periods, and a random effect to account for overdispersion in the data. We used

169   normally distributed prior distributions (mean = 0, sd = 1) for all fixed effects and uniform (0-10)

170   distributions for all standard deviation terms. We ran 5 MCMC chains using the default samplers

171   in the *nimble* package (NIMBLE development team 2021) for 500,000 iterations with a burn-in

172   of 300,000 iterations and thinned chains by 15. We ensured adequate MCMC mixing and

173   convergence by examining trace plots and tested for model fit using posterior predictive checks

174   based on Freeman-Tukey discrepancy measures (Table S1).

175   The coefficient for begging playback estimated for each species was used as a measure of

176   parental responsiveness to begging in all subsequent comparative analyses. We evaluated

177   hypotheses about the evolution of parental responsiveness to begging using the entire marginal

178   posterior distribution for β_{beg} to fully account for uncertainty in these estimates for each species.

179   Thus, we ran all models described below on each MCMC sample and we made inferences based

180   on the posterior probability of direction (pd), 95% highest density credible intervals, and region

181   of practical equivalence tests (ROPE) from the full distribution of results for each model (see

182   below for details).

183   We examined the association of parental responsiveness with site, adult survival rate, nest

184   predation rate, attrition rate, and nestling mass using separate phylogenetic generalized least

185   squares (PGLS) models in the package 'ape' (Paradis & Schliep 2018). These models describe

186   correlations between the variables of interest, but do not allow inference on the causal processes

187   that created the data or account for causal relationships between the variables. We also ran

188   generalized least squares models using the most probable posterior value of β_{beg} for each species

189   weighted by the sample size and we depict the results of these models in Figure 2.

190   To determine the causal drivers of parental responsiveness to begging, we used

191   phylogenetic path analysis (PPA; von Hardenberg & Gonzalez-Voyer 2013). PPA uses the d-

192   separation method to test the plausibility that a causal model created the observed data and to

193   compare the relative support of multiple models using an information theoretic approach. We

194   developed 15 possible models that described the direct effects of annual adult survival rate, nest

195   predation rate, brood attrition rate, and nestling mass on parental responsiveness to begging

196   playback as well as likely causal relationships between these variables. For example, since

197   nestling mass and nest predation rate are both likely influenced by adult mass (Mouton & Martin

198   2019), each model describes the effect of adult mass on nestling mass and nest predation rate.

199   We tested each of k conditional independencies of each model using phylogenetic least-squares

200   regression (PGLS), implemented in the package 'phylopath' (van der Bijl 2018). We tested the

201   plausibility of each causal model with P-values based on Fisher's C statistic, which follows a

202   chi-squared distribution with 2k degrees of freedom. We used the C statistic Information

203   Criterion with a correction for small sample sizes (CICc) to rank and compute the probability of

204   each causal model and variable given the data and the candidate model set (CIC weight;

205   Anderson et al. 2000; von Hardenberg & Gonzalez-Voyer 2013). We also report ROPE tests for

206   the probability that a model fit poorly (i.e. $p(P < 0.1)$) and the probability that a model was

207   among the best supported (i.e. $p(\Delta CICc < 2)$). Finally, we estimated model averaged path

208   coefficients to assess the effect of each variable on parental responsiveness across all MCMC

209   iterations where a model was well supported (i.e. $\Delta CICc < 2$).

210   Phylogenetic trees were acquired from birdtree.org (Jetz et al. 2012) using the Hackett

211   backbone (Hackett et al. 2008). We sampled a distribution of 1000 trees and produced majority-

212   rules consensus trees using program Mesquite (Fig. S1; Maddison & Maddison 2011). We log-

213   transformed adult and nestling body mass to meet model assumptions. All analyses were

214   conducted using program R (R core team, 2020)

215

216   **Results:**

217   Parents generally increased feeding visits to nests when experimental begging

218   vocalizations were being broadcast relative to controls, but the magnitude of responses differed

219   among species (Fig. 1; Std. dev.: Median = 0.082, 95% HDI = 0.003 – 0.174). Average parental

220   responsiveness to begging did not differ between the two field sites (PGLS: Median β_{Site} =

221   0.079, 95% HDI = -0.194 – 0.717, pd = 0.72) or among species based on adult survival rates

222   (Fig. 2A; PGLS: Median $\beta_{AdultSurvival}$ = -0.013, 95% HDI = -0.128– 0.107, pd = 0.58). However,

223   species with greater nestling predation rates (Fig. 2B; PGLS: Median $\beta_{NestPredation}$ = 0.084, 95%

224   HDI = -0.049 – 0.219, pd = 0.90), smaller nestling mass (Fig. 2C; PGLS: Median β_{mass} = -0.103,

225   95% HDI = -0.103 – 0.067, pd = 0.88) and greater brood attrition were more responsive to

226   begging (Fig. 2D; PGLS: Median $\beta_{Attrition}$ = 0.091, 95% HDI = -0.065 – 0.247, pd = 0.89).

227   Numerous causal models could have plausibly created the results. The model including

228   only the direct effects of nestling mass on parental responsiveness to begging was plausible

229   across the entire posterior distribution and was generally among the top models (p(P < 0.05) = 0;

230   p(ΔCICc < 2) = 0.77; Table 1; Fig. 3). The models including only the direct effect of nestling

231   attrition (p(P < 0.05) = 0.04; p(ΔCICc < 2) = 0.55; Table 1) or nest predation risk (p(P < 0.05) =

232   0.09; p(ΔCICc < 2) = 0.34; Table 1) alone were also plausible across most parameter values and

233   were often among the best supported models. The model including only the direct effect of adult

234   survival was plausible across most of the posterior, but was only rarely among the best supported

235   models (p(P < 0.05) = 0.15; p(ΔCICc < 2) = 0.14; Table 1). All remaining causal models were

236   poorly supported (p(ΔCICc < 2) = 0; Table S2).

237   Model averaging indicated essentially no effect of adult survival on parental

238   responsiveness (Fig.3; standardized path coefficient: Median = 0.00, 95% HDI = -0.097 – 0.076,

239   pd = 0.45), but provided moderate evidence for an effect of nestling mass (Fig.3; standardized

240   path coefficient: Median = -0.18, 95% HDI = -0.63 – 0.064, pd = 0.92), nestling attrition (Fig.3;

241   standardized path coefficient: Median = 0.13, 95% HDI = -0.05 – 0.53, pd = 0.91), and nest

242   predation rate (Fig.3; standardized path coefficient: Median = 0.10, 95% HDI = -0.062 – 0.449,

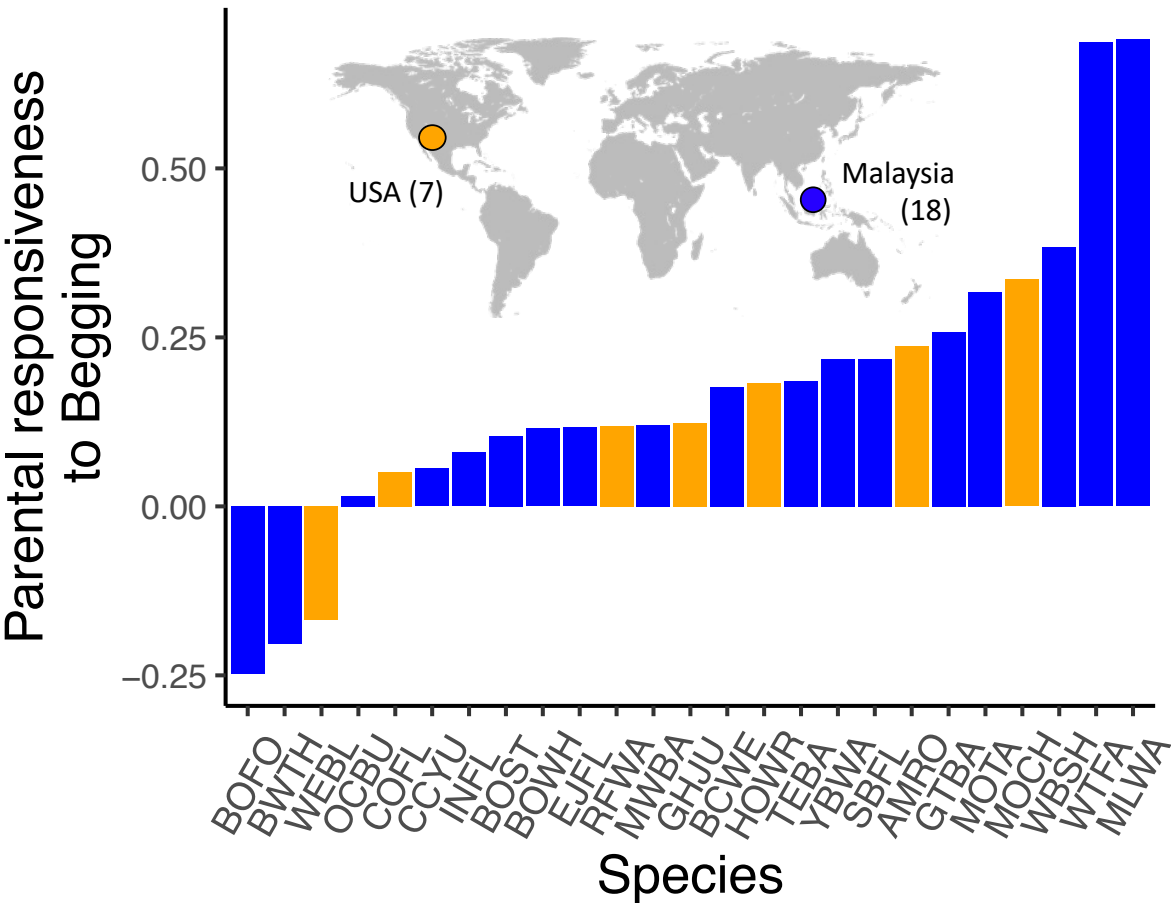243   pd = 0.92).

Figures:

Fig. 1: Variation in parental responsiveness to begging playback across species from tropical

(blue bars) and north temperate (orange bars) field sites. Blue bars depict most probable values

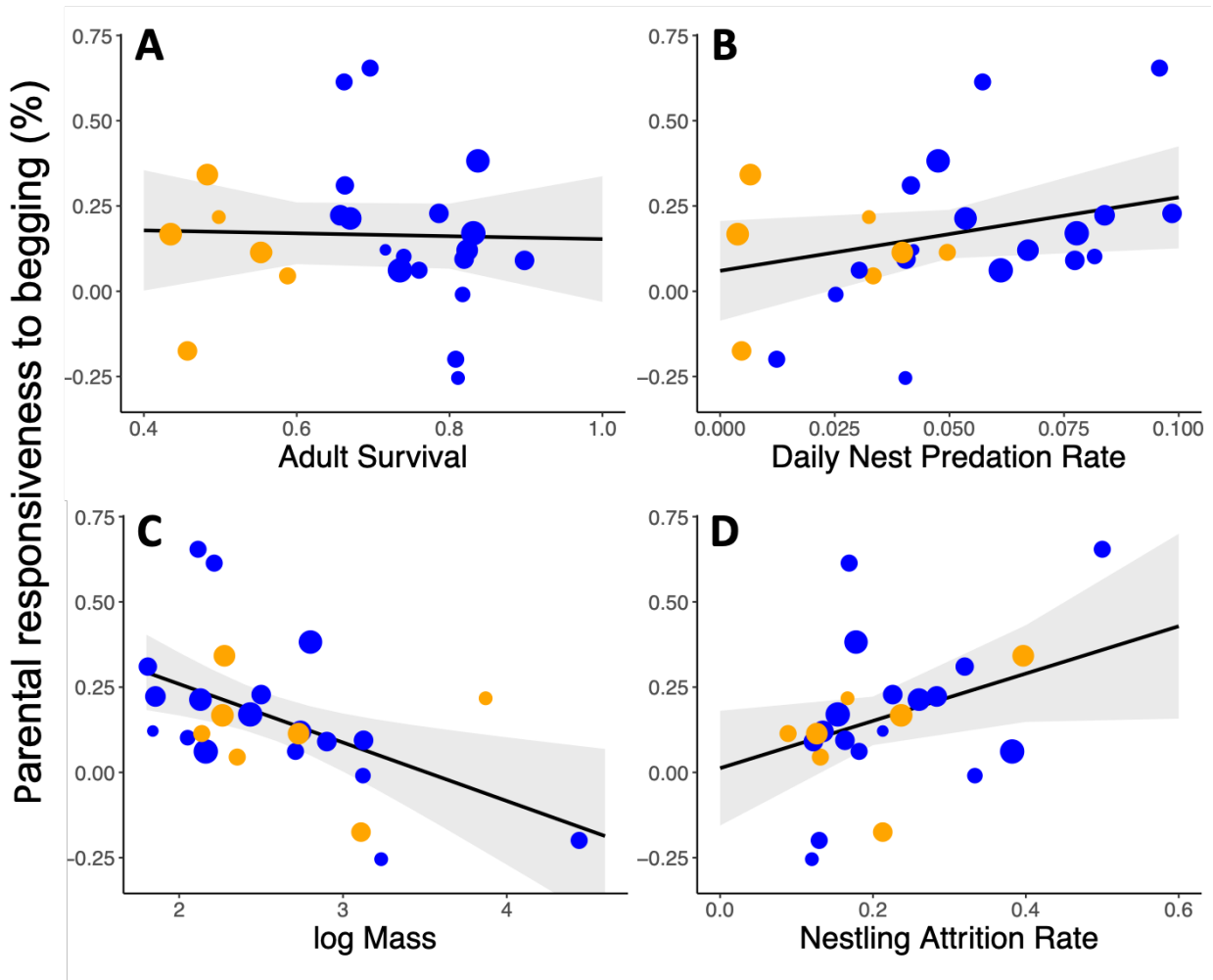of the posterior distribution. Species names are listed in Table S1.

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Fig. 2: Plots showing relationships between parental responsiveness to begging and **(A)** annual adult survival rate, **(B)** nest predation rate during the nestling stage, **(C)** nestling mass, and **(D)** nestling attrition rate. Data from the tropical Malaysia site are depicted in blue and data from the north temperate Arizona, USA site are depicted in orange. The size of points is proportional to the experimental sample size for each species. Trend lines and 95% confidence intervals (shaded regions) are based on a generalized linear model for each variable weighted by sample size for each species.
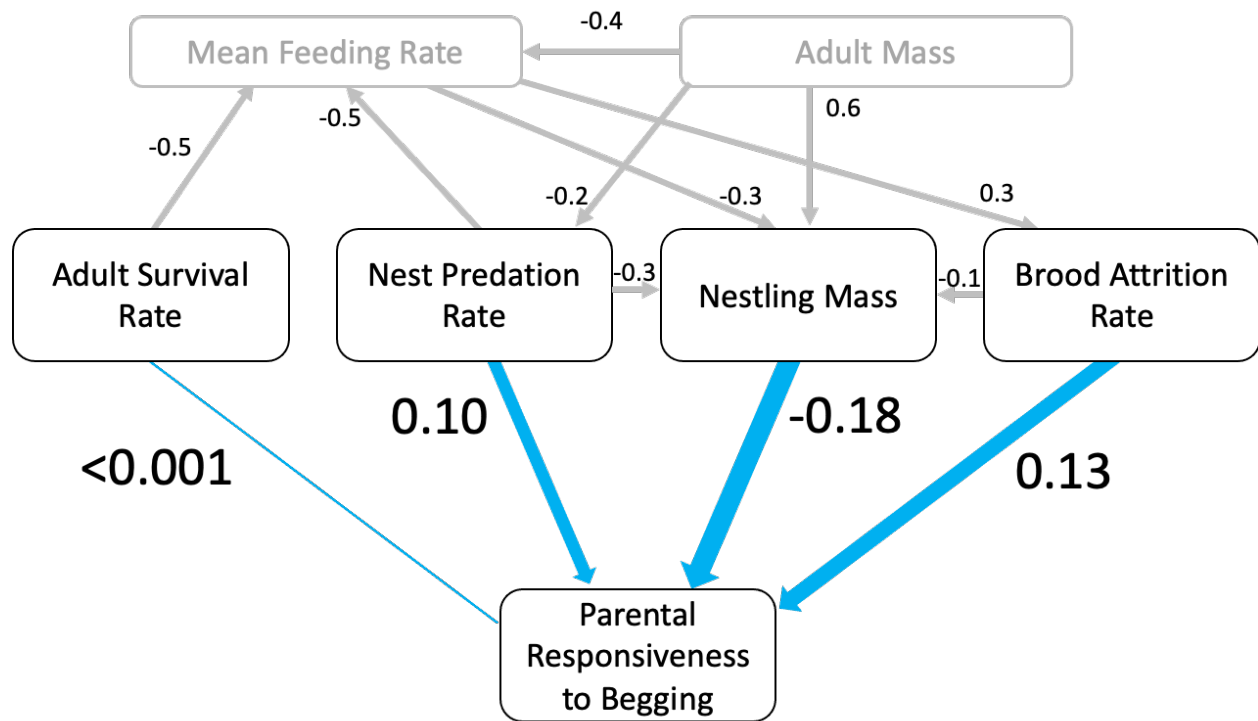
260

Fig. 3: Model averaged path coefficients illustrating the central hypotheses tested in blue and
other relationships between variables in gray.

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264

Tables:

Table 1: Posterior summaries from phylogenetic path analysis indicating the variables posited to have direct causal effects on parental responsiveness to begging for each model. *p*-values are based on Fischer's C statistic. Low *p*-values indicate models could not have plausibly created the data. We also report the difference in C statistic Information Criterion with a correction for small sample sizes (CICc) between models (ΔCICc) and the CICc weight of each model. Region of Practical Equivalence tests show the percentage of the 95% credible intervals indicating poor model fit (e.g. $p < 0.05$) or highly supported models (ΔCICc < 2). We include all models within 10 ΔCICc of the top model. Other causal models are presented in the supplementary material (Table S2).

Model	P value			Δ CICc			CICc Weight	
	Median	95% HDI	p(P < 0.05)	Median	95% HDI	p(ΔCICc < 2)	Median	95% HDI
Nestling Mass Only	0.432	0.066 - 0.793	0	0.000	0 – 6.223	0.77	0.407	0.04 – 1.00
Brood Attrition Only	0.363	0.011 - 0.730	0.040	1.794	0 – 9.499	0.55	0.213	0 – 0.854
Nest Predation Only	0.275	0.000 - 0.667	0.086	3.767	0 – 12.237	0.34	0.094	0 – 0.675
Adult Survival Only	0.201	0.000 - 0.625	0.154	5.776	0 – 13.345	0.14	0.035	0 – 0.282

Discussion:

Understanding which ecological factors drive the diversification of parental care
strategies is a major goal in evolutionary ecology (Clutton-Brock 1991; Royle et al. 2012).
Parental responsiveness to offspring solicitation behaviors is a parental care trait that is thought
to vary among species and has clear implications for fitness in both offspring and parental
generations. However, the underlying causes of this variation are unclear due to a focus on single
species and methodological differences among studies. Using standardized field experiments
across species, we found that variation in parental responsiveness to begging varies greatly
across species. Our experimental study suggests that parental responsiveness to begging is driven
largely by variation in ecological factors related to the energetic needs of young and average
offspring predation risk, and appears to be independent of adult survival rates.

In support of the *energetic requirements hypothesis*, species with smaller nestling mass
were more responsive to begging. Our comparative results agree with an experiment in house
sparrows (*Passer domesticus*) which suggested that parental responsiveness balanced the risk of
wasting time returning too soon to feed already satiated young against the risk of failing to feed
young in need (Grodsinski & Lotem 2007). Larger species with larger nestling body sizes were
associated with greater energetic stores and reduced mass specific metabolism across species
(Ton & Martin 2015), and may allow longer intervals between feedings with minimal risk to
offspring quality or survival. In contrast, parents may view begging calls with greater urgency in
smaller species with fewer energetic stores and higher mass specific metabolism. Overall,
parental responsiveness to begging seems to be greater in species where begging is more likely
to signal greater imminent costs for young based on energetic storage capacity and metabolic
requirements.

301   Increased begging intensity may also signal greater need in species with more

302   unpredictable food resources. In contrast to the *environmental predictability* hypothesis and

303   previous work focusing on allocation of care among nestmates (Caro et al. 2016), we found that

304   species with higher levels of brood attrition tend to be more responsive to begging calls. Parents

305   are unable to directly assess the likely outcomes of current vs. future broods because

306   environmental conditions may be unpredictable across seasons or breeding attempts. Due to this

307   uncertainty, species with more unpredictable food supplies may respond readily to increased

308   begging signals if food is currently abundant and increased provisioning is possible to decrease

309   the odds that young die if conditions deteriorate in the future. The interactions between strategies

310   for decisions about allocating provisioning among broods vs. among individual offspring within

311   broods (e.g. Caro et al. 2016) deserves more study. Ultimately, increased parental responsiveness

312   to begging in species with high brood attrition may reflect parents' efforts to maximize the

313   likelihood that current young survive.

314   We also found support for the idea that species at higher risk of predation are more

315   responsive to offspring solicitation, which may reflect a response to reduce the likelihood of

316   predators discovering nests using begging calls (*blackmail hypothesis*). However, previous single

317   species studies have given mixed results. Some bird species with relatively high nest predation

318   rates were highly responsive to experimentally augmented nestling begging calls (Price 1998;

319   Tarwater et al. 2009). Yet other species with similarly high predation rates showed very little

320   parental responsiveness (Clark & Lee 1998). Moreover, a cavity nesting species with very low

321   nest predation rates readily responded to increased begging playback (Hinde & Kilner 2007).

322   Sensory biases among common nest predators may determine the importance of offspring

323   predation risk as a driver of parental responsiveness to begging across species. In both Malaysia

324 and Arizona, common nest predators are likely able to cue into nests using both auditory and

325 visual cues (e.g. red squirrels (*Tamiasciurus hudsonicus)*, stellar's jays (*Cyanocitta stelleri*),

326 mountain tree shrew (*Tupaia montana*), bornean green-magpies (*Cissa jefferyi*); Mouton &

327 Martin 2019). So, selection for faster parental feeding responses to silence loud begging may be

328 partially offset by the fact that nest predation risk also selects for reduced visitation (Martin

329 2015). Communities dominated by nest predators with either auditory or visual sensory biases

330 may face more directional selection on parental responsiveness to begging and the acoustic

331 characteristics and modality of begging calls themselves (e.g. frequency, bandwidth, mouth

332 flush; Kilner 1997; Briskie et al. 1999). Together, our results highlight the potential importance

333 of predation costs of begging in the evolution of parent-offspring communication.

334   Our result that adult survival was not a major driver of variation in parental

335 responsiveness across species was surprising. The intensity of parent-offspring conflict is

336 expected to increase with adult survival rates and influence parental provisioning among species

337 (Kilner & Hinde 2008). Nonetheless, our results are bolstered by single species studies that used

338 similar experimental methods (Clark & Lee 1998; Price 1998; Tarwater et al. 2009; Haff &

339 MacGrath 2011). For example, the western slaty antshrike (*Thamnophilus atrinucha*) has high

340 adult survival, but was highly responsive to begging playback (Tarwater et al. 2009). Meanwhile,

341 the relatively short-lived red-winged blackbird (*Agelaius phoeniceus*) did not increase

342 provisioning with a similar playback experiment (Clark & Lee 1998). Our results also show that,

343 at least in the short term, shorter-lived species may not necessarily be working closer to maximal

344 capacity compared to longer-lived species with small brood sizes. Residual reproductive value

345 may still place a ceiling on the total amount of care parents will provide over longer periods of

346   time (Martin 1987, 2014). However, in the short term, our results show that adult survival

347   probability does not strongly influence parental responses to offspring begging.

348   Other ecological traits may also drive variation in parental responsiveness to offspring

349   begging. For example, species that raise young cooperatively in groups might be expected to be

350   more responsive overall because the costs of increasing provisioning are divided among multiple

351   individual caregivers. Moreover, cooperative breeding may also help reduce predation risk

352   because more caregivers can more easily detect nearby predators. Unfortunately, our study only

353   included 2 species that are cooperative breeders so we lack the ability to test this hypothesis

354   directly. However, cooperative breeding may not have strong effects on parental responsiveness.

355   Mountain Wren-Babblers (MWBA; *Napothera crassa*) and Chestnut-Crested Yuhinas (CCYU;

356   *Yuhina everetti*) are cooperative breeders (Kaiser et al. 2019; Slevin et al 2020) and both have

357   somewhat average parental responsiveness to begging (Fig. 1). Since non-parental caregivers in

358   cooperatively breeding species are less related to young than parents (e.g., Kaiser et al. 2019), it

359   is possible that reduced costs associated with cooperative breeding may be offset by reduced

360   benefits from providing care. Future studies could examine how variation in group size as well as

361   differing degrees of relatedness within cooperatively breeding species influences responsiveness

362   to begging.

363   The level of parental care provided to offspring is a major component of life history

364   strategies across taxa with critical implications for fitness (Williams 1966; Charlesworth 1994;

365   Roff 2002). Offspring can influence the level of parental care they receive using solicitation

366   displays, but parental responsiveness to solicitation displays varies across species. Here we

367   provide evidence that the energetic needs of offspring, environmental predictability, and

368   offspring predation risk drive this variation across diverse species. In contrast, we found little

369 evidence that variation among species in adult survival drive the evolution of parental

370 responsiveness to offspring begging. The widespread expression of offspring solicitation

371 behaviors across taxa begs for studies examining the evolutionary drivers of parental

372 responsiveness in other systems and contexts.

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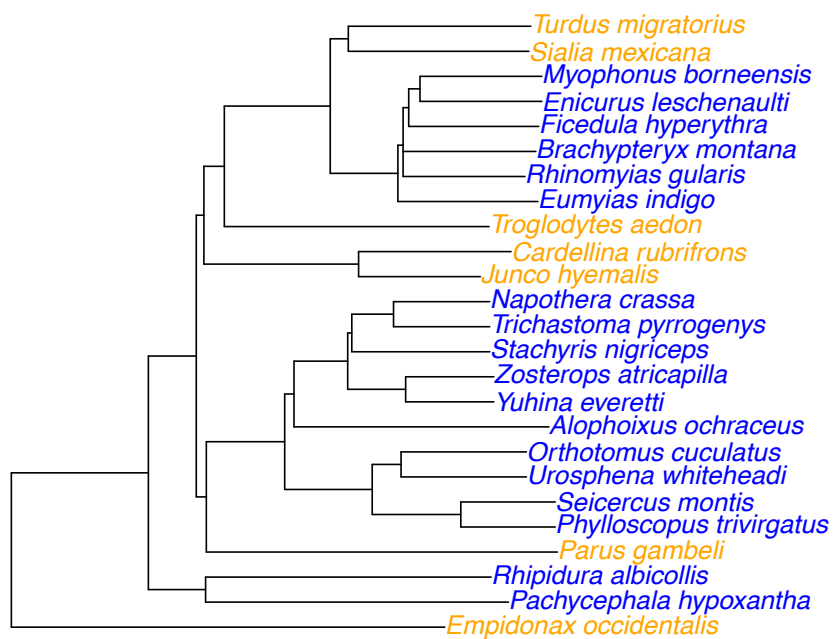
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484   **Supplementary Material:**

485   **Table S1:** Posterior summary for β_{beg}, life history data, number of experimental trials (N) and a

486   metric of model fit (Bayesian P-value) for each species. We present the most probable posterior

487   value (MAP), median, 95% highest density intervals, and the probability of direction (pd).

Latin	SPP	β_{beg}				Nest Predation	Brood Attrition	Adult Survival	Nestling Mass	Adult Mass	Mean Feeding Rate	Site	N	P
		MAP	Median	95% HDI	pd									
Empidonax occidentalis	COFL	0.05	0.05	-0.27 - 0.40	0.64	0.03	0.13	0.59	2.35	10.90	19.95	AZ	5	0.54
Rhipidura albicollis	WTFA	0.61	0.69	-0.43 - 1.81	0.90	0.06	0.17	0.66	2.21	12.53	16.35	MY	5	0.52
Pachycephala hypoxantha	BOWH	0.12	0.12	-0.28 - 0.50	0.73	0.07	0.13	0.82	2.74	22.77	4.57	MY	9	0.54
Parus gambeli	MOCH	0.34	0.34	-0.09 - 0.79	0.94	0.01	0.40	0.48	2.28	11.55	19.82	AZ	9	0.47
Stachyris nigriceps	GTBA	0.23	0.26	-0.33 - 0.87	0.82	0.10	0.23	0.79	2.50	15.89	3.88	MY	7	0.57
Trichastoma pyrrogenys	TEBA	0.17	0.18	-0.23 - 0.60	0.82	0.08	0.15	0.83	2.43	19.43	4.51	MY	12	0.70
Napothera crassa	MWBA	0.09	0.12	-0.53 - 0.83	0.65	0.08	0.12	0.90	2.90	28.70	4.31	MY	7	0.53
Yuhina everetti	CCYU	0.06	0.06	-0.31 - 0.40	0.63	0.06	0.38	0.74	2.16	13.15	8.09	MY	12	0.34
Zosterops atricapilla	BCWE	0.12	0.17	-1.14 - 1.68	0.63	0.04	0.21	0.72	1.84	8.98	11.09	MY	2	0.55
Alophoixus ochraceus	OCBU	-0.01	0.02	-0.66 - 0.70	0.52	0.03	0.33	0.82	3.12	48.65	5.03	MY	4	0.66
Urosphena whiteheadi	BOST	0.10	0.10	-0.58 - 0.84	0.62	0.08	0.13	0.74	2.05	10.41	6.62	MY	4	0.64
Orthotomus cuculatus	MOTA	0.31	0.32	0.04 - 0.61	0.98	0.04	0.32	0.66	1.81	7.02	16.80	MY	6	0.46
Phylloscopus trivirgatus	MLWA	0.65	0.69	-0.30 - 1.69	0.93	0.10	0.50	0.70	2.12	9.47	5.68	MY	5	0.54
Seicercus montis	YBWA	0.22	0.22	-0.27 - 0.73	0.83	0.08	0.28	0.66	1.85	6.65	12.26	MY	8	0.48
Troglodytes aedon	HOWR	0.17	0.18	-0.03 - 0.40	0.96	0.00	0.24	0.44	2.26	10.77	21.08	AZ	10	0.53
Turdus migratorius	AMRO	0.22	0.24	-0.88 - 1.31	0.67	0.03	0.17	0.50	3.87	77.30	6.23	AZ	3	0.71
Sialia mexicana	WEBL	-0.17	-0.17	-0.46 - 0.14	0.87	0.00	0.21	0.46	3.11	27.00	17.78	AZ	7	0.57
Rhinomyias gularis	EJFL	0.09	0.12	-0.52 - 0.79	0.65	0.04	0.16	0.82	3.13	26.33	5.42	MY	7	0.65
Brachypteryx montana	WBSH	0.38	0.38	0.05 - 0.70	0.99	0.05	0.18	0.84	2.80	20.56	5.72	MY	11	0.60
Ficedula hyperythra	SBFL	0.21	0.22	-0.27 - 0.71	0.83	0.05	0.26	0.67	2.13	8.66	14.25	MY	10	0.52
Enicurus leschenaulti	BOFO	-0.25	-0.25	-0.97 - 050	0.79	0.04	0.12	0.81	3.23	38.29	7.59	MY	3	0.57
Myophonus borneensis	BWTH	-0.20	-0.20	-0.87 - 0.47	0.74	0.01	0.13	0.81	4.44	126.23	3.51	MY	5	0.69
Eumyias indigo	INFL	0.06	0.08	-0.39 - 0.58	0.65	0.03	0.18	0.76	2.71	16.01	8.68	MY	5	0.53
Junco hyemalis	GHJU	0.11	0.12	-0.22 - 0.47	0.77	0.04	0.13	0.55	2.73	20.94	7.48	AZ	9	0.70
Cardellina rubrifrons	RFWA	0.11	0.12	-0.51 - 0.70	0.68	0.05	0.09	0.56	2.14	9.77	9.02	AZ	5	0.52

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489

490　**Table S2:** Posterior summaries from phylogenetic path analysis indicating the variables posited

491　to have direct causal effects on parental responsiveness to begging for each model. *p*-values are

492　based on Fischer's C statistic. Low *p*-values indicate models could not have plausibly created the

493　data. We also report the difference in C statistic Information Criterion with a correction for small

494　sample sizes (CICc) between models (ΔCICc) and the CICc weight of each model. Region of

495　Practical Equivalence tests show the percentage of the 95% credible intervals indicating poor

496　model fit (e.g. $p < 0.05$) or highly supported models (ΔCICc < 2).

Model	P value			Δ CICc			CICc Weight	
	Median	95% HDI	ROPE (0-0.05)	Median	95% HDI	ROPE (0-2)	Median	95% HDI
Nestling Mass Only	0.432	0.066 – 0.793	0	0.000	0 – 6.223	0.77	0.407	0.04 – 1.00
Brood Attrition Only	0.363	0.012 – 0.730	0.040	1.794	0 – 9.499	0.56	0.213	0 – 0.854
Nest Predation Only	0.275	0.000 - 0.667	0.086	3.770	0 – 12.24	0.34	0.094	0 – 0.675
Adult Survival Only	0.201	0.000 – 0.625	0.155	5.780	0 – 13.34	0.14	0.036	0 – 0.282
Nestling Mass + Brood Attrition	0.451	0.070 – 0.770	0	27.75	23.51 – 32.53	0.00	0.000	0 - <0.001
Adult Survival + Nestling Mass	0.370	0.022 – 0.715	0.023	28.58	21.52 – 37.92	0.00	0.000	0 - <0.001
Brood Attrition + Nest Predation	0.366	0.030 – 0.722	0.016	28.75	23.23 – 35.44	0.00	0.000	0 - <0.001
Nest Predation + Nestling Mass	0.353	0.029 – 0.718	0.019	29.00	23.84 – 35.41	0.00	0.000	0 - <0.001
Adult Survival + Brood Attrition	0.333	0.004 – 0.694	0.054	29.15	23.68 – 37.36	0.00	0.000	0 - <0.001
Adult Survival + Nest Predation	0.285	0.000- 0.653	0.070	30.08	24.63 – 38.32	0.00	0.000	0 - <0.001
Nest Predation + Nest Mass + Brood Attrition	0.396	0.068 – 0.713	0	66.42	61.27 – 72.31	0.00	0.000	0 - <0.001
Adult Survival + Nest Mass + Brood Attrition	0.396	0.030 – 0.698	0.015	66.61	59.35 – 74.50	0.00	0.000	0 - <0.001
Adult Survival + Nest Predation + Nestling Mass	0.414	0.083 – 0.712	0	66.63	59.90 – 71.16	0.00	0.000	0 - <0.001
Adult Survival + Nest Predation + Brood Attrition	0.374	0.046 – 0.695	0.003	67.22	61.06 – 72.02	0.00	0.000	0 - <0.001
Adult Survival + Nest Mass + Brood Attrition + Nest Predation	0.442	0.145 – 0.666	0	124.17	118.4 – 128.0	0.00	0.000	0 - <0.001

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499   **Figure S1:** Majority-rules consensus tree for 25 species from Arizona (orange) and Malaysia

500   (blue) field sites.

501