Fear affects parental care, which predicts juvenile survival and exacerbates the total cost of fear on demography

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Abstract. Fear itself (perceived predation risk) can affect wildlife demography, but the cumulative impact of fear on population dynamics is not well understood. Parental care is arguably what most distinguishes birds and mammals from other taxa, yet only one experiment on wildlife has tested fear effects on parental food provisioning and the repercussions this has for the survival of dependent offspring, and only during early-stage care. We tested the effect of fear on late-stage parental care of mobile dependent offspring, by locating radio-tagged Song Sparrow fledglings and broadcasting predator or non-predator playbacks in their vicinity, measuring their parent's behavior and their own, and tracking the offspring's survival to independence. Fear significantly reduced late-stage parental care, and parental fearfulness (as indexed by their reduction in provisioning when hearing predators) significantly predicted their offspring's condition and survival. Combining results from this experiment with that on early-stage care, we project that fear itself is powerful enough to reduce late-stage survival by 24%, and cumulatively reduce the number of young reaching independence by more than half, 53%. Experiments in invertebrate and aquatic systems demonstrate that fear is commonly as important as direct killing in affecting prey demography, and we suggest focusing more on fear effects and on offspring survival will reveal the same for wildlife.

Key words: anti-predator behavior; dependent offspring; ecology of fear; perceived predation risk; post-fledging survival; predator–prey interaction.

Introduction

Predators kill dependent young but the responses of parents to predators could conceivably be a key driver of offspring mortality as well, though the cumulative impact that fear might have on prey population dynamics in wildlife is not well understood. To grow and survive, offspring of course need to eat, and for most species of birds and mammals, food intake is entirely dependent on parental food provisioning. As such, the extent and/or quality of parental care can either cause offspring to thrive or it could literally kill them (Royle et al. 2012). The perceived risk of predation is well known to alter foraging decisions such that scared prey typically eat less (reviews in Lima 1998, Caro 2005, Stankowich and Blumstein 2005), but manipulations in wildlife showing that predator-induced alterations in parental food provisioning can be powerful enough to affect the mass and survival prospects of dependent offspring are few. The only experiment to date is by Zanette et al. (2011) who broadcast predator or non-predator playbacks to manipulate fear, and measured the effects on parental care (food provisioning rate) and the survival of dependent offspring in Song Sparrow (*Melospiza melodia*) nests. Frightened parents provisioned their young 26% less frequently with the result that 20% fewer of their offspring survived to

fledging (leaving the nest). This reduction in offspring survival coupled with fewer eggs laid and more hatching failure meant that frightened parents produced nearly 40% fewer offspring over the breeding season. Though this fear effect on demography is quite intense, the total cost of fear on offspring production could be even greater than what Zanette et al. (2011) reported if predator-induced reductions in food provisioning extend into the period of late-stage care, when offspring are mobile (i.e., ambulant) but still fully dependent on their parents for food. Indeed, the juvenile stage per se has been identified as being particularly important to the population dynamics of wildlife because yearly variation in the population growth rate for many birds and mammals is largely driven by juvenile survival (Gaillard et al. 1989, Dybala et al. 2013, Gaillard and Yoccoz 2003, Reid et al. 2011, Bjørkvoll et al. 2016). In fact, the precise timing at which juvenile survival can create a demographic bottleneck evidently occurs primarily during the period of late-stage care, which sets the ceiling on the number of offspring available to recruit (reviewed in Cox 2014).

Late-stage parental care of mobile dependent offspring can involve more than simply food provisioning. Offspring typically need to learn how to forage, and what to fear (i.e., which animals are predators, what cues signal the presence of predators, and how to respond), some of which they may learn from their parents (Mainwaring 2016, Stockley and Hobson 2016). Mobile dependent offspring may conceivably show reduced survival caused by their parent's fright, but also their own of fearlessness (if,

for example, offspring are naive to predators), and the two may frequently be interlinked. In both birds and mammals, offspring commonly vocalize (beg) or otherwise make themselves conspicuous to signal their hunger and so elicit food provisioning from parents (Godfray 1991, Kilner and Hinde 2012). Fearful parents may be expected to provision less, which could cause young to make themselves more conspicuous and which may also make them more conspicuous to predators (Haff and Magrath 2011).

Some means of tracking mobile dependent offspring is necessary to quantify both late-stage parental care and offspring survival during this important life-history stage, and this generally requires using radio or satellite transmitters (Mainwaring 2016). New technologies have made tracking mobile dependent offspring more feasible in recent years, but the newness of these technologies means comparatively few studies have yet addressed how variation in late-stage parental care affects offspring development (Naef-Daenzer and Grüebler 2016, Stockley and Hobson 2016), and no study has yet experimentally tested the effects of fear.

To gain a comprehensive understanding of the total effect that fear can have on prey populations, we experimentally tested the effect of fear on late-stage parental care of mobile dependent offspring and assessed whether parental fearfulness (responsiveness to perceived predation risk) was predictive of their offspring's condition (mass) and subsequent survival. Working in the same system studied by Zanette et al. (2011), we located radio-tagged Song Sparrow fledglings, broadcast predator or non-predator playbacks in their vicinity and assessed the effect on their parent's behavior and their own, and subsequently tracked the survival of these offspring to shortly after independence. We then used these results to make projections regarding the potential effect of fear on juvenile survival in the population as a whole. We then combined these results with those of Zanette et al. (2011) to make population projections regarding the cumulative effect of fear on offspring production and juvenile survival, and hence the total effect of fear on the number of juveniles reaching independence. Our results indicate that the effect of fear on late-stage parental care of mobile dependent offspring may be stronger than the effect on early-stage care previously demonstrated, potentially at least doubling the cumulative impact of fear on the survival of dependent offspring. We discuss why a greater focus on testing fear effects on dependent offspring in experiments on birds and mammals may provide the most productive means of establishing whether, as in invertebrates and amphibians, fear may frequently be as, or more, important than direct killing in affecting the demography of wildlife.

Materials and Methods

Study area and species

We studied wild Song Sparrows resident on several small (<200 ha) Gulf Islands, in British Columbia, Canada, from March to September 2014, as part of a long-term project. Study locations do not vary significantly in terms of predation risk, and this and other details regarding sites and sparrows can be found elsewhere (Zanette et al. 2011). Four stages of parental investment and care may be readily distinguished in this species: (1) parental investment in egg production (fecundity), the duration of egg-laying being determined by the number of eggs laid (from 1 to 5); (2) pre-natal parental care, encompassing the incubation of eggs from laying to hatch (13 d); (3) early-stage parental care of dependent offspring, comprising the period from hatch to fledging (10–12 d); and (4) late-stage parental care of mobile dependent offspring, encompassing the period between fledging and independence (which we define as 21 d). Both parents contribute to early- and late-stage care and parents can successfully rear two or three broods to independence in a breeding season.

Overview of experimental design and demographic projections

We radio-tagged nestling Song Sparrows during brood-rearing, midway through the early-stage of parental care (6 d after hatching), weighing them immediately prior to tagging to quantify their condition. To quantify their condition upon the completion of early-stage care we recaptured them within hours of their having fledged (left the nest) and weighed them again.

We radio-tracked the now mobile offspring on the third day after fledging and, upon locating them, conducted a 2 h long repeated-measures experiment to test the effect of fear on their parent's behavior and their own. We positioned three speakers around the offspring, each 8 m from its location (following Ghalambor et al. 2013), and an equal distance apart. We then broadcast predator calls for 1 h, followed after 15 min by 1 h of non-predator calls, or vice versa, balancing the order of treatment presentation among offspring. During the playbacks, an observer, positioned 8 m from the offspring, recorded the number of times the parents visited the offspring to provision it and the number of times it was fed, how concealed the offspring kept itself between parental visits, the height above ground of the perches it used, and the distance it moved and amount it begged over the course of each treatment hour. Immediately following the completion of the 2 h long experiment we additionally assessed the offspring's flight initiation distance (FID) (Stankowich and Blumstein 2005, Zanette et al. 2011). Following this, we radio-tracked these same offspring every second day to determine if it survived to shortly after independence, and if not, at what age it died. Upon each check, survival or death was definitely confirmed by seeing the offspring alive or retrieving its corpse.

To assess whether parental fearfulness (responsiveness to perceived predation risk) was predictive of their offspring's condition and survival, we used an index of parental fearfulness. Here, we calculated the reduction in

food provisioning visits during the predator playbacks compared to during the non-predator playbacks, such that the greater the relative reduction in parental visits during the predator treatment (i.e., the greater the number above zero), the more fearful the parents. Using this index we quantified the relationship between parental fearfulness and their offspring's prior condition (mass on day 6 post-hatch and fledge-day); their offspring's subsequent survival to shortly after independence; and age of death if they did not survive.

Zanette et al. (2011) reported that fear effects on early-stage parental provisioning affects offspring condition and survival to fledging. If parents are consistently fearful, being equally responsive to predator cues during early- and late-stage care, their fearfulness at the late-stage may be expected to be correlated with their offspring's prior (early-stage) condition. Early-stage offspring condition can have life-long effects in Song Sparrows (MacDonald et al. 2006, Zanette et al. 2009), including potentially affecting survival to independence. Because the adaptive function of parental care is to improve offspring survival (Alonso-Alvarez and Velando 2012), then one might expect that the offspring's early-stage condition would not be the sole determinant of its subsequent survival, and that late-stage parental care will moderate the effect of prior condition. That is, prior condition and later care will interact in affecting the survival of late-stage dependent offspring. We correspondingly tested whether offspring's prior condition (on day 6 post-hatch and fledge-day) interacted with late-stage parental fearfulness (as indexed by our experiment) in affecting the offspring's subsequent survival to independence.

Zanette et al.'s demonstration that fear itself can reduce early-stage offspring survival by 20% involved comparing between two treatment groups; individuals that heard predator playbacks and others that heard non-predator playbacks, broadcast throughout the period of early-stage care (brood rearing). Zanette et al. assessed (1) the mean effect of fear on parental provisioning on day 5 of brood rearing; (2) the correlation between individual variation in this measure of parental care and offspring survival to fledging; and (3) the mean effect of fear on offspring survival to fledging. Our experiment provided us with data on (1) the mean effect of fear on parental provisioning on day 3 of late-stage (i.e., post-fledging) care and (2) the correlation between individual variation in this measure of care and offspring survival to independence, permitting us to (3) project the mean effect of fear on survival to independence, which may be expected if playbacks were broadcast to separate predator and non-predator treatment groups throughout the entire period of late-stage care, similar to what Zanette et al. did for early-stage care. Projecting this mean effect provides an estimate of the potential population-level effect of fear on the survival of mobile dependent offspring. Mathematically this simply entailed using the equation for a logistic regression derived from the correlation between parental fearfulness (reduction in provisioning in response to predator playbacks)

and offspring survival to independence (probability of survival = $1/(1 + e^{0.309x-1.687})$, where x is the reduction in provisioning, and 0.309 and −1.687 are the slope and intercept respectively, see *Results*).

As noted in the *Introduction*, Zanette et al. (2011) reported that fear itself not only reduced early-stage offspring survival, but fecundity and hatching success as well; with the cumulative effect that frightened parents fledged 40% fewer young. To estimate the total effect of fear on the number of young reaching independence we multiplied the negative effect size of fear on the number fledging (−40%) by our projected estimate of the mean effect size of fear on offspring survival from fledging to independence, calculated as described in the previous paragraph.

Field procedures, playbacks, and behavioral measures

Offspring mass was measured to 0.01 g using a digital scale (Model PPS200; Pesola AG, Switzerland). Radio-tags (PicoPip Ag317; Biotrack, Wareham, UK) weighing 0.35 g (<3% of body mass) were fitted to day 6 post-hatch nestlings using a leg loop harness (Rappole and Tipton 1991). We tagged two nestlings per nest, balancing the assignment of tags by rank order of body mass in nests with more than two nestlings to ensure our overall sample of tagged nestlings included a balanced number of lightweight, middleweight, and heavy nestlings. Only one tagged offspring from each nest was targeted in our 2 h long experiment, and we balanced which of the two was targeted such that one-half of the trials were on the lighter, and one-half on the heavier of the two. Forty-four offspring were targeted in total, 30 from first (early-season) and 14 from second (late-season) broods, the parents of each brood being different in the great majority of cases (89%).

To manipulate fear, we composed separate playlists of the calls of either predators (Common Raven, *Corvus corax*; Cooper's Hawk, *Accipiter cooperii*; Merlin, *Falco columbarius*; Sharp-shinned Hawk, *Accipiter striatus*) or non-predators (Canada Goose, *Branta canadensis*; Northern Flicker, *Colaptes auratus*; Black Oystercatcher, *Haematopus bachmani*; Hairy Woodpecker, *Picoides villosus*) all observed at our study sites. Each predator was matched with a similar-sounding non-predator (e.g., raven caw with goose honk), and analyses verified that there were no significant differences in overall frequency characteristics between the two treatments (peak, $t_7 = -1.2$, $P = 0.26$; minimum, $t_7 = -0.3$, $P = 0.80$; maximum, $t_7 = -1.6$, $P = 0.16$; range, $t_7 = 0.3$, $P = 0.75$). We used five exemplars of each species (obtained from the Cornell Lab of Ornithology and Borror Laboratory of Bioacoustics) to compose two, 1-h randomized playlists. Playbacks were broadcast at a volume of 80 dB at 1 m, using mp3 players (Prism; Hip Street Canada, Toronto, Ontario, Canada) plugged into the three speakers (Ecoextreme; Grace Digital, San Diego, California, USA) arrayed around the target offspring. The three units each

broadcast randomly but were programmed such that in aggregate the ratio of sound to silence was 1:1.5 (following Zanette et al. 2011).

All behavioral measures recorded during the 2 h long experiment were made by a single observer (B. P. Dudeck) who dictated them into a voice recorder (ICD-PX333; Sony of Canada, Toronto, Ontario, Canada) while simultaneously recording all offspring vocalizations (begging calls) using a high-quality digital audio recorder with omnidirectional microphones (Tascam DR-05; TEAC America, Montebello, California, USA). Parental behaviors measured included the number of times the parents visited the offspring to feed it, the number of times it was fed upon each visit (multiple food items often being brought to their young by Song Sparrow parents; Pagnucco et al. 2008, DeCaire et al. 2013), and the total number of times the offspring was fed during each 1-h treatment period. How concealed the offspring kept itself between parental visits was quantified by recording if it was visible or not, every 10 min, at which time the height above ground of the perch it was on was also estimated, to the nearest 1 m. The distance the offspring moved was quantified by two means: (1) measuring the straight-line distance (m) between its position at the beginning and end of each 1-h playback treatment and (2) estimating the distance it moved within each 2-min interval during each 1-h treatment and calculating the median "step" distance. The number of begging calls offspring made when the parents were present, and the number made when they were absent (Platzen and Magrath 2004), was transcribed from the recordings made during each treatment period. Flight initiation distance was measured as the horizontal distance (cm) between the offspring and the observer when the offspring fled, upon the approach of the observer (following Zanette et al. 2011).

Statistical analyses

We conducted repeated-measures ANOVAs comparing responses between the predator and non-predator playback periods, to test the effects of our experiment on all parental and offspring behaviors, except for flight initiation distance, which was analyzed using a single-measure ANOVA as this was only measured once at the end of each 2-h long experiment. We included brood number (first or second) and playback order (whether predators or non-predators were heard first) in these ANOVAs, but only report treatment effects in the *Results*, because there were no significant main effects or interactions associated with these other factors (all $P > 0.30$).

To test if parental fearfulness during late-stage care was correlated with their offspring's prior (early-stage) condition, we conducted a repeated-measures ANCOVA with our index of parental fearfulness as the covariate and offspring mass on day 6 post-hatch and fledge day as the repeated measures. To determine if parental fearfulness predicted their offspring`s subsequent survival we conducted a logistic regression testing the correlation

between parental fearfulness and whether their offspring survived to independence. We further tested whether age at death, among those that died, was associated with parental fearfulness using a Spearman rank correlation test. To corroborate that fear effects on the amount of food offspring were provided during late-stage care affected their survival, we conducted logistic regressions testing the relationship between the offspring's survival to independence and (1) the reduction in the total amount of food it received (i.e., reduction in the total number of times fed) during the predator compared to the non-predator treatment; and (2) the interaction between prior (early-stage) condition and parental fearfulness.

We repeated the above analyses either including parental identity as a random effect in linear mixed models, or excluding the handful of cases ($n = 5$) where parental identity was not unique (though of course, the identity of the offspring was unique), and as neither of these procedures affected which variables were identified as significant, we report values only from the more straightforward analyses already discussed. Prior to analysis, all data were tested for normality and homogeneity of variances and where necessary were Box-Cox transformed (Krebs 1999) or assessed using a non-parametric test. All descriptive results reported (means $\pm$ SE) are untransformed or back transformed to the original units.

RESULTS

Fear significantly affected late-stage parental care. Hearing predator playbacks caused parents to reduce the number of food provisioning visits they made to their mobile dependent offspring by 37% relative to hearing non-predator playbacks (Fig. 1; $F_{1,41} = 22.49$, $P < 0.001$). Parents also fed their offspring significantly fewer times per visit when hearing predators (30% fewer; predator, 0.89 ± 0.08; non-predator, 1.27 ± 0.04; $F_{1,41} = 29.02$, $P < 0.001$). The net result of being visited less and fed less per visit was that offspring were fed 44% fewer times in total when parents heard predators (predator, 6.90 ± 0.83; non-predator, 12.34 ± 0.92; $F_{1,42} = 44.31$, $P < 0.001$).

Hearing predator calls had no significant effect on any measure of offspring behavior (all $P > 0.14$), indicating that offspring did not respond to these cues of apparent imminent danger their parents so strongly responded to. Indeed, because offspring in no way moderated their begging vocalizations between the two treatments (predator, 210 ± 44 vocalizations/h; non-predator, 194 ± 33 vocalizations/h; $F_{1,16} = 0.33$, $P = 0.57$) meant that a significantly greater proportion of the offspring's calls were made when it was alone, in the absence of their parents (predator, 0.69 ± 0.05; non-predator, 0.44 ± 0.05; Wilcoxon $T_{21} = 20.0$, $P < 0.001$), making itself conspicuous to any predator in the vicinity, at the very time it was actually hearing predator calls.

Parental fearfulness during late-stage care was significantly inversely correlated with their offspring's prior,
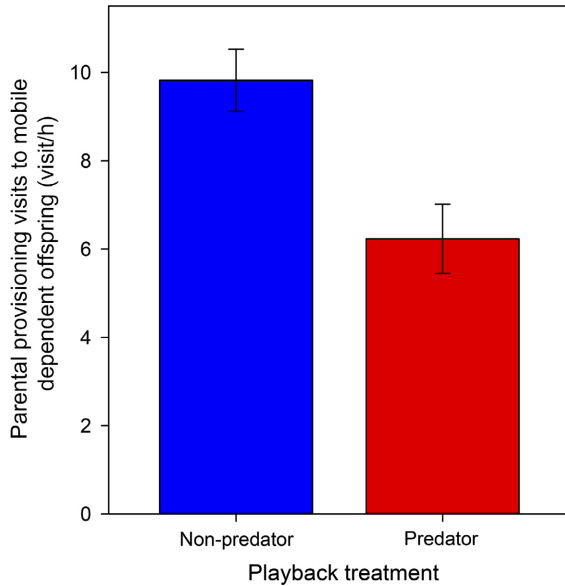
FIG. 1. Effect of predator (red) and non-predator (blue) playbacks on the number of provisioning visits parents made to their offspring. Values are means ± SE.

early-stage condition (Fig. 2; mass on day 6 post-hatch and fledge day; $F_{1,36} = 5.12$, $P = 0.030$), in addition to their offspring's subsequent probability of survival to independence (Fig. 3; Wald $\chi^2 = 4.26$, $P = 0.039$,

$b = 0.309 \pm 0.147$). Corroborating the causality between parental fearfulness and offspring fate, parental fearfulness was also significantly inversely correlated with offspring age of death, among those that died; more fearful parents had offspring that died at a younger age (Spearman $r_s = -0.62$, $P = 0.023$). That fear effects on the amount of food provided during late-stage care affected offspring survival was corroborated by a significant inverse correlation between the reduction in the total amount of food the offspring was fed during the predator treatment and its subsequent survival (Wald $\chi^2 = 5.17$, $P = 0.023$). Finally, parental fearfulness during late-stage care did evidently moderate the effects of early-stage condition because offspring survival was predicted by a significant interaction (Wald $\chi^2 = 4.71$, $P = 0.030$). Specifically, offspring were more likely to die if they were both lighter early-on and had more fearful parents during late-stage care, but were more likely to survive if they were both heavier early-on and had less fearful parents during late-stage care.

Using the observed relationship between parental fearfulness and offspring survival to independence (regression line in Fig. 3), and the observed mean reduction in food provisioning in response to hearing predator playbacks (3.6 visits/h; see Fig. 1), we projected that the probability of offspring survival to independence would be 64% (Fig. 3) if predator playbacks were broadcast throughout the period of late-stage care vs. 84% if they had heard non-predator sounds (Fig. 3). The resulting
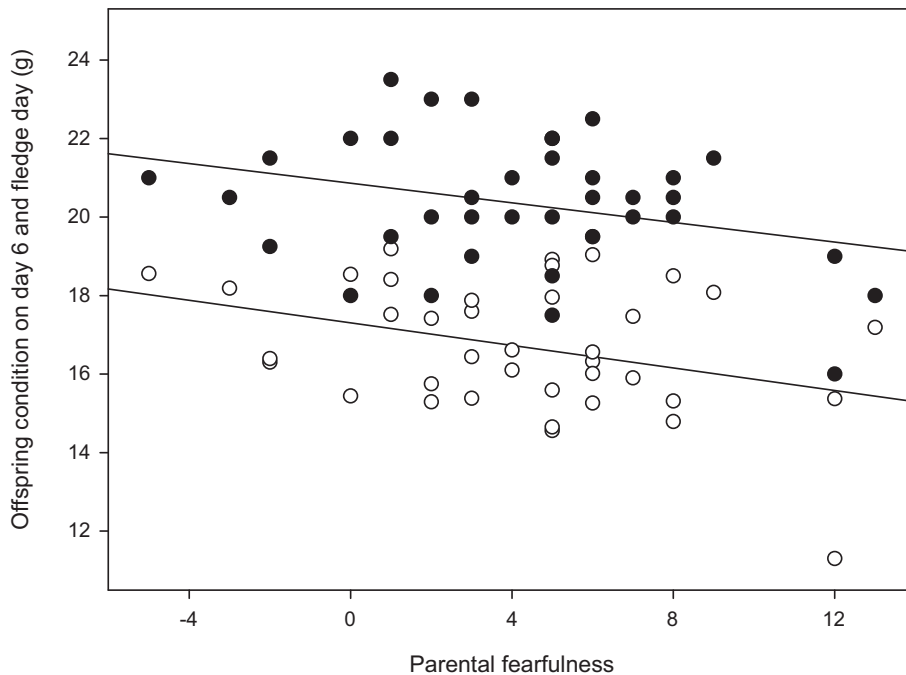

FIG. 2. Relationship between parental fearfulness, as indexed by their reduction in provisioning visits when hearing predators, and their offspring's condition (mass) as measured on day 6 post-hatch (open circles) and fledge day (solid circles). Parental fearfulness is indexed as the reduction in food provisioning visits during the predator playbacks compared to during the non-predator playbacks, such that the greater the number above zero, the more fearful the parents.
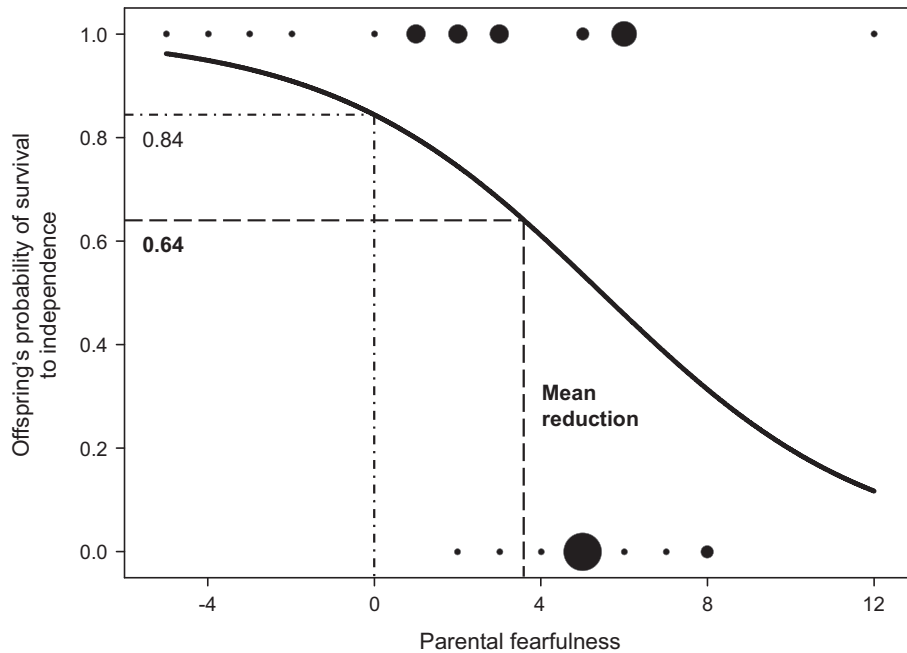
Fig. 3. Relationship between parental fearfulness as indexed by the reduction in provisioning visits when hearing predators, and their offspring's survival to independence (solid circles; the relative size of the circle signifying the relative number of offspring to which the given value of parental fearfulness and survival applied). The curved line illustrates the regression from the logistic equation. The dashed line shows the projected effect on survival of prolonged exposure to predator cues, given the mean reduction in provisioning visits in response to predator cues documented in our experiment (from Fig. 1). The dot-dashed line indicates the projected survival if only non-predators were heard.

relative reduction in offspring survival would therefore amount to 24% (survival probability in the non-predator minus the predator treatments divided by the non-predator treatment). This relative reduction of 24% thus constitutes our estimate of the mean effect of fear on the survival of mobile dependent offspring, to be expected from conducting an experiment comparable to Zanette et al.'s (2011). Combining this projected estimate of the mean effect of fear on offspring survival from fledging to independence with the cumulative negative effect of fear on the number of offspring fledging (−40%) demonstrated by Zanette et al. (2011), we estimate that fear may more than halve (−53%) the number of young reaching independence.

Discussion

Our results experimentally demonstrate that fear of predators impairs late-stage parental care and does so to an even greater degree than during early-stage care, as the reduction in food provisioning visits we documented (37%; Fig. 1) exceeded that in Zanette et al.'s (2011) experiment on early-stage care (26%). Our results additionally indicate that parental fearfulness affects offspring condition (Fig. 2), as did Zanette et al. Most importantly, at the population level, our experiment indicates that, by feeding their mobile dependent offspring less, fearful parents cause a 24% reduction in the

survival of their offspring (Fig. 3). This additional cost of fear in combination with that reported by Zanette et al. (2011) indicates that fear itself (i.e., simply hearing the sound of predators) is powerful enough to reduce the number of young reaching independence by more than one-half (53%).

That our index of parental fearfulness predicted offspring survival (Fig. 3) is readily understandable. The danger posed by the predators whose calls were broadcast is very real given that all are present at our study sites and kill both adults and juveniles (Zanette et al. 2011, Rodewald 2015). Our experiment assayed the responses to cues indicative of a predator's immediate presence. We therefore, simulated responses to situations the subjects would undoubtedly have experienced in reality on numerous occasions (i.e., hearing predator calls), throughout the period of late-stage parental care; the consequences of such responses evidently resulting in real effects on offspring survival. On the flip-side, if the effect of parental fearfulness on offspring survival is the result of parents sacrificing their offspring's survival to ensure their own, as the parent–offspring conflict literature would suggest (Alonso-Alvarez and Velando 2012, Kilner and Hinde 2012), then the relationship between parental fearfulness and parental survival may be expected to be the opposite of that observed for offspring (Fig. 3). That is, more fearful parents should be more likely to survive. On the other hand, the food

intake of parents themselves can be inhibited by predator-induced fear (reviews in Lima 1998, Caro 2005, Stankowich and Blumstein 2005, Zanette et al. 2013) and can additionally degrade the physiological condition of breeding females (Zanette et al. 2013), which could decrease survival rates. How these two forces might balance out would have to be quantified, which could be accomplished by radio-tagging and tracking the adults.

Our projection regarding the potential overall demographic effect of fear on the survival of mobile dependent offspring to independence (−24%) assumes that parents subject to prolonged exposure to predator cues (e.g., over the course of late-stage care) would continue to respond as strongly as they did in our 2 h long experiment. The evidence to date supports this assumption. Parents in Zanette et al.'s experiment continued to respond to predator playbacks broadcast for 130 d. In a related experiment on raccoons (Suraci et al. 2016) it was directly verified that the immediate, short-term responses to predator playbacks were comparable to those exhibited after 30 d of playback exposure. Our projected 24% relative reduction in survival is also based on what would be expected if we had broadcast predator calls at the same rate as Zanette et al. (2011). This is a reasonable assumption because those authors showed that their playback design well-simulated natural differences in exposure to predator cues, because it generated demographic effects comparable in magnitude to those documented in comparisons between areas naturally varying in predator abundance (Zanette et al. 2003).

Whereas parents in our experiment responded strongly to predator cues, their offspring did not. It is likely that the fearfulness of parents combined with their offspring's fearlessness (e.g., naiveté) affected offspring survival (Godfray1991, Haff and Magrath 2011, Kilner and Hinde 2012). In the presence of predator sounds, offspring continued to make themselves conspicuous (beg) even during the parents' prolonged absences, which itself was due to the parents' perception of immediate risk (hearing predators). Offspring may be expected to learn what is fearful over the course of late-stage care (Mainwaring 2016, Stockley and Hobson 2016), and prolonged exposure to predator cues could conceivably accelerate this learning. However, other experiments we have conducted, manipulating provisioning (MacDonald et al. 2006) and fear (using predator playbacks; Zanette et al., *unpublished data*), indicate that predator-induced reductions in parental food provisioning may be expected to permanently impair the offspring's ability to learn. Moreover, a poor rearing environment induced by fear could mean that any surviving offspring might recruit as poor quality adults with relatively low reproductive success, which could further erode the population growth rate (Albon et al. 1987, Lindström 1999, Reid et al. 2003, Bian et al. 2015).

Our results reinforce that fear effects on parental care can affect the survival of dependent offspring, with potentially dramatic impacts on the demography of wildlife (Zanette et al. 2011). Although adult survival may vary with parental fearfulness, the life history of birds and mammals would suggest that the magnitude of any such effect on demography would be far less than the effects that fear has on offspring survival. Birds and mammals have a life history that is frequently characterized as "slow" relative to other taxa (i.e., invertebrates, amphibians, fishes), with high adult survival and low fecundity, and among-year variation in adult survival is generally far less than offspring survival. Moreover, among-year variation in the population growth rate is typically driven primarily by the recruitment (survival) of young (Gaillard et al. 1989, Gaillard and Yoccoz 2003, Jeschke and Kokko 2009, Reid et al. 2011, Bjørkvoll et al. 2016).

Fear has been demonstrated to be as, or more, important than direct killing in affecting prey demography in numerous experiments on invertebrates and amphibians conducted almost exclusively in mesocosms (Preisser et al. 2005, 2007, 2009). Many fewer manipulations have been done on free-living wildlife (birds and mammals) but the evidence to date demonstrates that fear also affects these prey populations (Eggers et al. 2006, Sheriff et al. 2009, Travers et al. 2010, Zanette et al. 2011, 2013, Hua et al. 2014, LaManna and Martin 2016). Meta-analyses of the many experiments on invertebrates and amphibians indicate that fear affects demography primarily through fecundity (the number of propagules produced; Preisser et al. 2005, 2007, 2009). Fear effects on the survival of propagules/offspring that depend on their parents for care have largely been unconsidered in these studies because of the life history of the taxa under consideration; parental care is a rarity in invertebrates (Trumbo 2012), frogs, and fishes (Balshine 2012). In contrast, parental care may be described as a fundamental feature of the life history of birds and mammals; mammals are defined by the fact they express milk to feed their dependent young, and virtually all birds provide some parental care (Royle et al. 2012, Stockley and Hobson 2016). Yet there is a near absence of experiments testing fear effects on the survival of dependent offspring in birds and mammals, which is at odds with the important role parental care plays in these taxa. Most fear manipulations on wildlife have examined the effects of fear on fecundity, possibly because of the focus on fecundity in the invertebrate and amphibian literature. Aside from Zanette et al. (2011) ours is the only other experiment examining fear effects on the survival of dependent young. However, it is the survival of dependent young that is evidently particularly affected by fear and as such would contribute most to the growth rate of prey populations. For example, fear had a relatively modest 8% effect on fecundity (eggs laid) in Zanette et al.'s (2011) experiment, and thus contributed only very modestly to our projection that fear can more than halve (−53%) the number of young reaching independence, and similarly modest effects on fecundity are the norm in the handful of fear experiments on wildlife.

Interestingly, fear effects on fecundity (see Cherry et al. 2016) are at the core of the controversy concerning the reintroduction of wolves to Yellowstone National Park and whether this has affected the pregnancy rate in elk (Creel et al. 2007, Middleton et al. 2013a, b). All authors agree that calf recruitment has declined, but somewhat surprisingly, it has not to our knowledge been considered that this could in part be attributable to a reduction in calf survival resulting from fear effects on parental care (Creel et al. 2007, Griffin et al. 2011, Middleton et al. 2013a, b). In a classic experiment, Berger et al. (2001) broadcast predator playbacks to moose mothers, demonstrating that this increased their vigilance and reduced their foraging. Berger et al. did not report measuring the effect on nursing (parental care) but this would seem to be a straightforward behavior to add when monitoring the mother's vigilance and foraging. Given the evident effectiveness of using predator playbacks to assay the responses of large ungulates, we suggest the most feasible first step in testing if fear affects calf survival in large ungulates would be to assay parental fearfulness and determine if this predicts offspring survival, in the same fashion as we have done here. If this is the case, the next step would be to conduct a prolonged playback manipulation, to experimentally verify that fear effects on parental care affects the survival of mobile dependent offspring in large ungulates (Moll et al. 2017).

Fear effects on the physiology and behavior of prey are universal, leading one to expect fear effects on demography to be universal as well (Lima 1998). The specific behaviors and specific demographic parameters affected may of course vary among taxa. Our research and that of others has demonstrated that fear itself is powerful enough to affect wildlife population dynamics (Eggers et al. 2006, Sheriff et al. 2009, Travers et al. 2010, Zanette et al. 2011, 2013, Hua et al. 2014, LaManna and Martin 2016), and our results here point to the effects of fear being even more dramatic. For researchers, conservationists and managers interested in testing if fear effects on the demography of wildlife can be as powerful as shown in invertebrate and aquatic systems (Preisser et al. 2005, 2007, 2009), we suggest that while we should model our experiments on the extraordinary work accomplished in these systems, we should focus more on the behavior (parental care) and consequent life history component (survival of dependent offspring) that distinguishes birds and mammals from other taxa.

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