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The influence of fledgling location on adult provisioning: a test of the blackmail hypothesis

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One theory to explain the existence of conspicuous solicitation is that it is a way for young to 'blackmail' carers into provisioning them, by threatening their own destruction. Fledgling birds offer a unique opportunity to investigate the 'blackmail theory', as their mobility enables them to influence the predation risk they face. We investigated a novel solicitation behaviour in fledgling pied babblers (*Turdoides bicolor*), where fledglings use their location to influence provisioning rates. We show that fledglings face a trade-off: the ground is a much more profitable location in terms of provisioning rate from adult carers, but they are at greater risk from predators owing to their limited flying ability and slow response to alarm calls. Young babbler fledglings move to the ground when hungry, signalling their state, and this stimulates adults to increase their provisioning rates. Once satiated, fledglings return to the safety of cover. By experimentally increasing terrestrial predation risk, we found that adults increased their provisioning rate to terrestrial but not arboreal fledglings. Thus, by moving to a riskier location, fledglings revealed their need and were able to manipulate adults to achieve higher provisioning rates. These results provide support for the 'blackmail theory'.

1. Introduction

Altricial young are dependent on adults to provide them with the necessary nutrition for growth and development [1]. The nutritional needs of altricial young may be cryptic and difficult for carers to determine [2,3], hence both carers and young will benefit from young communicating their need. Previous research has revealed that conspicuous solicitation behaviours have evolved in many species to enable dependent young to signal to and extract resources from carers (reviewed in [4]). However, owing to genetic asymmetries caused by sexual reproduction, theory predicts different optimal levels of investment for parents and offspring [5]. Parents and offspring are therefore predicted to 'disagree' over provisioning behaviour; a concept known as parent–offspring conflict (POC). POC has been the subject of much theoretical and empirical research in a variety of taxa (reviewed in [4,6]). Trivers [5] originally hypothesized that offspring use solicitation behaviours to manipulate parents into provisioning them at a higher level than is optimal for the parents. Zahavi [7] expanded on this concept by proposing that predation risk shapes parent–offspring interactions, suggesting that vocal begging is an attempt by offspring to 'blackmail' parents into provisioning them by the threat of their own destruction. Here, we empirically test Zahavi's theory in a novel social context.

When the production of solicitation displays imposes a cost on the signaller, the cost of the signal means the signal is more likely to be honest [2,8]. Two main costs have been put forward for solicitation behaviours [2]: energy expenditure and predation risk. The metabolic costs of begging have been investigated, with mixed results [9,10]. By contrast, predation risk has been shown to be a greater cost associated with begging: Haskell [11] showed that nestling birds

suffer a real risk of predation owing to begging, suggesting that predation risk may promote honesty in nestling begging signals [12].

The majority of theoretical and empirical studies of avian solicitation and POC have focused on nestlings [13], owing to the difficulties in observing fledglings [14]. However, the nestling and fledgling environments are qualitatively different: nestlings are in a fixed location, in close proximity to their siblings and have to wait for adults to return and provision them. By contrast, fledglings are mobile and able to follow adults to solicit food directly [15]. Fledgling predation risks are therefore different to those of nestlings, resulting in different mortality rates according to developmental stage [16,17]. During the nestling phase, offspring are a fixed source of noise that gradually gets louder during the nestling period [18], making them more conspicuous to predators [11]. By contrast, the mobility of fledglings means they are no longer a fixed source of noise, but can move in a three-dimensional environment [19,20], where predation risk can vary depending on their location [21].

The vulnerability of offspring to predation will depend critically on their ability to evaluate and respond to predation risk. The young of many species react to predation risk either by responding to adult alarm calls [17,22] or by assessing predation risk independently of cues/warnings from adults (reviewed in [20]). However, the response to predation risk is often poor or inappropriate in naive young [23], because perception of risk may often be dependent on past experience [24]. Offspring response to predators can also be limited by developmental constraints, such as limited physical capacity to evade predators [25].

All animals face a trade-off between food intake and anti-predation behaviour [24]. When offspring are directly dependent upon adult carers, those adults can be viewed as a food source or foraging patch. Fledglings may therefore face a trade-off between either following adult carers or remaining in safer, but less profitable locations, such as under the cover of trees or bushes [26]. This trade-off is particularly relevant for terrestrially foraging birds, whose main escape from predators is to flee to cover in bushes and trees [21,26]. If energetic rewards are greatest when following carers in locations of higher predation risk [27], fledglings face a trade-off between maximizing their growth rates and maximizing their survival. Therefore, we predict that the level of risk that fledglings are willing to tolerate will depend critically on their hunger level: hungrier fledglings should be willing to accept higher predation risk to achieve greater amounts of provisioning.

Pied babblers (*Turdoides bicolor*) fledge their young at a very immature stage—young are unable to fly for up to a week post-fledging and take a long time to develop adult-like mobility [28]. This poor mobility has the potential to put them at greater risk from predators compared with adult babblers, offering a unique opportunity to investigate post-fledging conflict over provisioning. Here, we investigate whether hungrier fledglings move to riskier locations to increase the amount of provisioning they receive from adults, presenting the opportunity to test Zahavi's [7] prediction that begging behaviour will be most effective in areas with high predation risk. To investigate the relationship between offspring solicitation, predation risk and adult provisioning, the threat of predation needs to be altered [12,29]. Through observations and experimental manipulations of predation risk, we determined (i) whether terrestrially located fledglings are at higher risk of predation; (ii) the optimal location for fledglings (terrestrial or arboreal) in terms of adult provisioning rates; and (iii) whether changes in predation risk cause adults to change their behaviour towards fledglings.

2. Material and methods

(a) Study site and species

We studied adult-fledgling interactions in 14 groups of pied babblers in the southern Kalahari Desert at the Kuruman River Reserve, South Africa (26.58° S, 21.49° E) between November 2009 and March 2012. Pied babblers are a cooperatively breeding passerine, where all adult group members contribute to the provisioning of nestlings and fledglings [30]. Pied babblers are predominantly terrestrial foragers, spending more than 95 per cent of their foraging time on the ground [31]. Young are unable to fly for up to a week post-fledging and are dependent upon adults for food for several months [32]. During the post-fledging dependent phase, fledglings actively follow and beg at foraging adults [15]. The babbler population at the study site has been habituated to close human presence (less than 2 m), enabling detailed behavioural observation (see [31] for details of habituation process). All birds were individually identifiable with a unique combination of coloured and metal rings. For a list of predators, see the electronic supplementary material.

(b) Data collection
(i) Behavioural data
General behavioural data were collected using the ad libitum method [33]. The behaviours recorded included: feeding events (identity of adult and chick, as well as food type and size), the location of the fledglings (ground or tree) and the duration (seconds) of all lead calls given by adults [30]. Food item sizes and weights were calculated using the same methods as [32]. Lead calls are used by adults to move fledglings from one location to another and to move them away from danger [30]. Lead call behaviour was deemed to have ceased when adults stopped emitting lead calls. We carried out over 208 h of field observations, encompassing 3177 feeding events. All ad libitum and focal data (see below) were recorded on a Palm T/X handheld personal digital assistant (Palm, Inc.; Sunnydale, CA, USA).

(ii) Response to alarm call experiment
To determine the speed of fledgling response to alarm calls, as a proxy for their vulnerability to predation, we simulated intense predator interactions by playing back pied babbler mobbing calls. Playbacks were created from recordings of natural mobbing events towards slender mongoose (*Galerella sanguinea*), made 10–15 m from the mobbing event. All playbacks were group-specific to avoid the group responding to the playback as if it were a neighbouring group. Playbacks were normalized to 85 dB and cut to 11 s long, to simulate natural mobbing alarms. Playbacks were conducted 10 m from the foraging group and only when at least one fledgling was located on the ground. To avoid groups habituating to playbacks, each playback was used only once and the gap between experiments at each group was one week. Playbacks were only conducted if the last major behavioural disturbance (predator alarm or inter-group interaction) was more than 30 min before. The response we recorded was movement to cover (as defined by [26]), as this is the normal response to this type of alarm call. The response time to the playback by the focal fledgling and the nearest adult (less than 1 m) to them was recorded (seconds), along with the distance of the fledgling from cover (metres).

(iii) Feeding experiment

To determine how hunger affected the location of fledglings, we compared their behaviour before and after supplementary feeding. All data (27 fledglings from 12 groups) were collected while offspring were dependent upon adult carers for food (age range 31–84 days post-hatching). We used detailed focal observations on individual fledglings lasting 20 min, during which all foraging events, begging events, feeding events (identity of feeder, and prey item type and size), lead calls (identity of caller, duration and context) and location (ground or tree) were recorded. A control focal was conducted on each fledgling, the fledgling was then fed 10 meal worms (*Tenebrio molitor*; approx. 4.5 g), and then a second 20-min focal was carried out. The biomass of supplementary food provided (approx. 4.5 g) amounted to approximately 2.5 times the biomass a fledgling would normally consume on average per 20 min (1.68 ± 0.059 g s.e., range 0–6.4 g), constituting biomass likely to satiate the fledgling. To account for any temporal effects, controls were also carried out (16 fledglings from 10 groups; age range 23–75 days post-hatching). The controls used the same methods as detailed above, except without supplementary feeding between focal observations.

(iv) Predator perception experiment

To determine whether an increase in perceived predation risk affected how adult pied babblers behaved towards fledglings, we manipulated the quantity of heterospecific alarm calls that the group overheard (similar to the technique used in previous studies [34,35]). We recorded natural mobbing events on slender mongoose by Cape glossy-starlings (*Lamprotornis nitens*) and white-browed sparrow-weavers (*Plocepasser mahali*), co-occurring heterospecific species. Using these recordings, we created experimental playbacks, normalized to 75 dB to mimic the volume of heterospecific alarm calls occurring in the *vicinity* of the group. Experimental playbacks comprised two 15 s bouts of mobbing separated by a 10 s bout of background noise. Control playbacks consisted of two 15 s bouts of contact calls (from the same heterospecific species) interspersed with 10 s of background noise. Six experimental and control exemplars were created. Experimental and control playbacks were paired and conducted on consecutive days, with the order randomized: individual experimental and control playbacks were never paired more than once. Ad libitum data were collected on each babbler group for 60 min. The first 30 min were the control for each treatment, and in the second 30 min a playback was conducted once every 10 min to simulate either an increased predation risk (experimental playback) or continuation of the same level of risk (control playback). Playbacks were carried out 10 m from the foraging group. All experiments were conducted on 30-day-old (approx. two weeks post-fledging) fledglings, to control for age. This age was chosen because fledglings start coming to the ground more frequently, yet are still poor fliers with slow alarm call response [30].

(c) Statistical analyses

All statistical analyses were conducted using GENSTAT 14th edn (VSN International, Rothamstead, UK). Linear mixed models (LMMs) were used to assess: (i) the difference in speed of response to alarm calls between adults and fledglings, (ii) provisioning rate to fledglings, and (iii) proportion of time fledglings spent on the ground. Details on the model selection method using Akaike's Information Criterion for small datasets (AICc; [36]) are included in the electronic supplementary material. Here, we report the effect size and Wald statistic (χ^2) for predictor variables included in the most parsimonious model of those we considered in each analysis.

Paired analyses were carried out on paired experimental data to investigate: (i) the effect of hunger on the amount of time that fledglings spent on the ground, and (ii) the effect of perceived
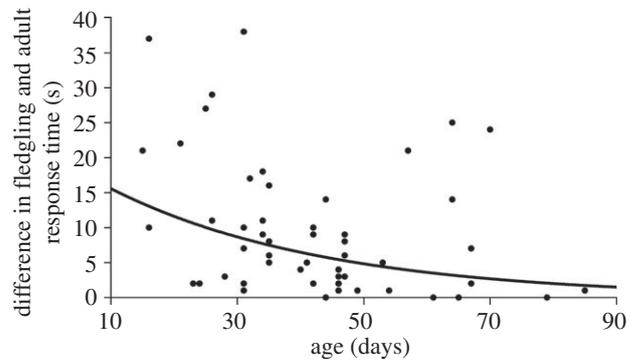
Figure 1. The relationship between age and response time to alarm calls. Response is defined as the time it takes a bird to reach cover after the start of the playback. The line shows the predictions from the best model investigating the difference in response time between fledglings and adults to alarm calls (see the electronic supplementary material, table S4; $n = 68$).

predation risk on (a) the percentage of time fledglings spent on the ground; (b) the provisioning rate to terrestrially located fledglings; (c) the provisioning rate to arboreally located fledglings; and (d) the proportion of time that adults spent giving lead calls to terrestrially located fledglings.

Tests for normality were conducted on all data. If data were non-normally distributed they were transformed: proportional data were arcsine square-root transformed, and non-proportional data were $\log_{10}$ or square-root transformed to achieve normality. If transformation did not result in a normal distribution, non-parametric tests were performed. Data are deposited in the Dryad repository (http://dx.doi.org/10.5061/dryad.5t1b5).

3. Results

(a) Fledgling response to alarm calls

The response of fledglings to the alarm calls of adult group members was initially poor, with a large difference between adult and fledgling response time (mean response times: fledglings 12.6 s (± 1.3 s.e.), adults 3.7 s (± 0.3 s.e.)). As fledglings aged, their response times to alarm calls increasingly converged on those of adults (see the electronic supplementary material, table S4a; LMM effect -0.013 ± 0.003, $\chi^2 = 25.65$; figure 1). The number of adults in the group also affected the alarm call response, with fledglings having a slower response in groups with more adults (see the electronic supplementary material, table S4a; LMM effect 0.167 ± 0.051, $\chi^2 = 10.57$). More than one model had $\Delta AICc < 5$; using predictor weights fledgling age and group size were the most important predictors of fledgling response time (see the electronic supplementary material, table S7).

(b) Where is the most profitable location for fledglings?
(i) Where do fledglings get provisioned the most?

The most significant factors that affected provisioning rates to fledglings were location and age. Fledglings were fed at a higher rate on the ground than in trees (mean provisioning rates: ground 0.12 g min^{-1} (± 0.008 s.e.), tree 0.03 g min^{-1} (± 0.002 s.e.; see the electronic supplementary material, table S5; LMM effect ground: 0.000 ± 0.000; tree -0.139 ± 0.013, $\chi^2 = 116.2$)). In general, provisioning rate decreased as fledglings became older (see the electronic supplementary

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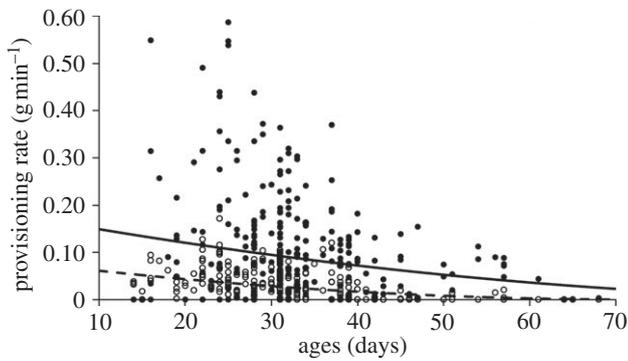
Figure 2. The effect of location on the relationship between age and provisioning rate (g min^{-1}) to fledglings. Lines show the predictions from the best model for provisioning rates on the ground (filled circles) and in the trees (open circles) related to age (see the electronic supplementary material, table S5). The solid line is the ground and the dashed line is for trees ($n = 472$).

material, table S5; LMM effect -0.004 ± 0.001, $\chi^2 = 44.19$; figure 2).

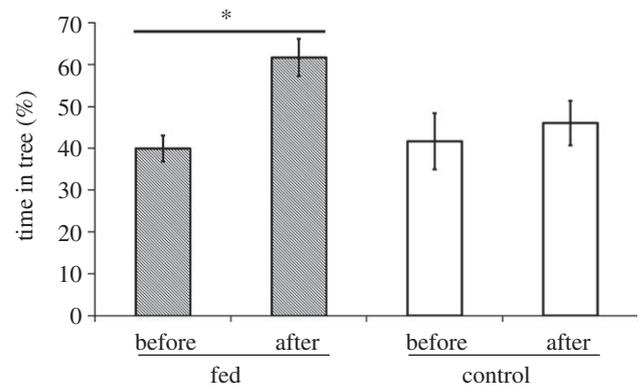### (ii) The effect of hunger on fledgling location

Fledgling hunger affected their location, with supplementally fed fledglings spending more time in trees (proportion of time in trees prior to supplementation: $39.9 \pm 3.1\%$ in trees, after supplementation: $61.7 \pm 4.4\%$ in trees, paired t-test, d.f. $= 37$, $p < 0.001$; figure 3). There was no significant difference in the proportion of time that control fledglings spent in the cover of trees between the before ($41.7 \pm 6.7\%$ in trees) and after focals ($46.0 \pm 5.3\%$ in trees, paired t-test, d.f. $= 17$, $p = 0.548$; figure 3).

(c) Responses to predation risk: heterospecific alarm calls

Control playbacks did not affect fledgling location (time on the ground (%)), terrestrial provisioning rate (g min^{-1}) to fledglings, arboreal provisioning rate (g min^{-1}) to fledglings or the percentage of time that adults spent giving lead calls to fledglings on the ground (see the electronic supplementary material, table S8; figure 4a–d). During playback of heterospecific alarm calls, we found no difference in the arboreal provisioning rate (g min^{-1}) to fledglings (see the electronic supplementary material, table S8; figure 4c). However, we did find a difference in location: fledglings spent less time on the ground (figure 4a). In addition, following alarm call playbacks, adults provisioned terrestrially located fledglings at a higher rate and invested more time in lead calling to terrestrially located fledglings (for all means $\pm$ s.e. and p-values, see electronic supplementary material, table S8; figure 4b,d). There was no difference in dominant and subordinate adults provisioning responses to either the control (paired t-test, d.f. $= 22$, $p = 0.064$) or experimental (paired t-test, d.f. $= 22$, $p = 0.112$) playbacks (see the electronic supplementary material, table S9 for means).

(d) Causes of variation in fledgling location

Overall, fledglings spent more time in the cover of trees than on the ground (tree: $76.64 \pm 1.34\%$ s.e.; ground: $23.34 \pm 1.34\%$ s.e.). However, this difference in location was strongly affected by fledgling age: young fledglings primarily spent their time in the cover of trees, whereas older fledglings


Figure 3. The effect of hunger on fledgling location. The effect of feeding experiment (feeding fledglings 10 meal worms) and the control on the percentage of time that fledglings spend in trees (means $\pm$ s.e.).

moved to the ground more often to beg from terrestrially foraging adults (see the electronic supplementary material, table S6; LMM effect 0.022 ± 0.001, $\chi^2 = 374.27$; figure 5). In addition, fledglings in groups with fewer adults spent more time on the ground than those with more adults (see the electronic supplementary material, table S5; LMM effect 0.039 ± 0.009, $\chi^2 = 19.84$). The total terrestrial and arboreal provisioning rates that fledglings received were all highly negatively correlated with fledgling age and positively correlated with number of adults in the group.

4. Discussion

In this study, we demonstrated that: (i) owing to slow response to alarm calls, young fledglings took longer to reach safety when on the ground than adults or older fledglings; (ii) fledglings received higher feeding rates from adults when on the ground than when in the cover of trees; and (iii) adults responded to higher perceived terrestrial predation risk by elevating their provisioning rates and investing more time in leading terrestrially located fledglings back to cover. As fledglings aged, they spent longer on the ground. This is probably owing to them responding faster to alarm calls and hence being at lower risk to predators. Combined, these results are consistent with Zahavi's [7] idea that, by increasing the risk of their own mortality, babbler fledglings can 'blackmail' adults into provisioning them at higher rates. Therefore, by moving to riskier locations when hungry, fledglings may exert a greater influence on adult provisioning rate.

There are several possible alternative explanations for adults provisioning terrestrial fledglings at higher rates: (i) fledglings on the ground are closer and therefore less costly to provision; (ii) hungrier fledglings approach adults, who happen to be on the ground, to solicit care and fledgling location is linked to adult location; (iii) terrestrially located fledglings beg more, thus eliciting higher provisioning rates; and (iv) movement to the ground by fledglings signals offspring quality (ability to evade predators). All hypotheses are plausible. For example, previous research has found that adults typically provision the closest offspring [15,37], and in many species, including pied babblers (A. M. Thompson 2013, unpublished data), hungrier offspring beg more (reviewed in [4]), and we have shown that less satiated fledglings spend more time on the ground. However, our experimental evidence indicates that these are unlikely explanations for the

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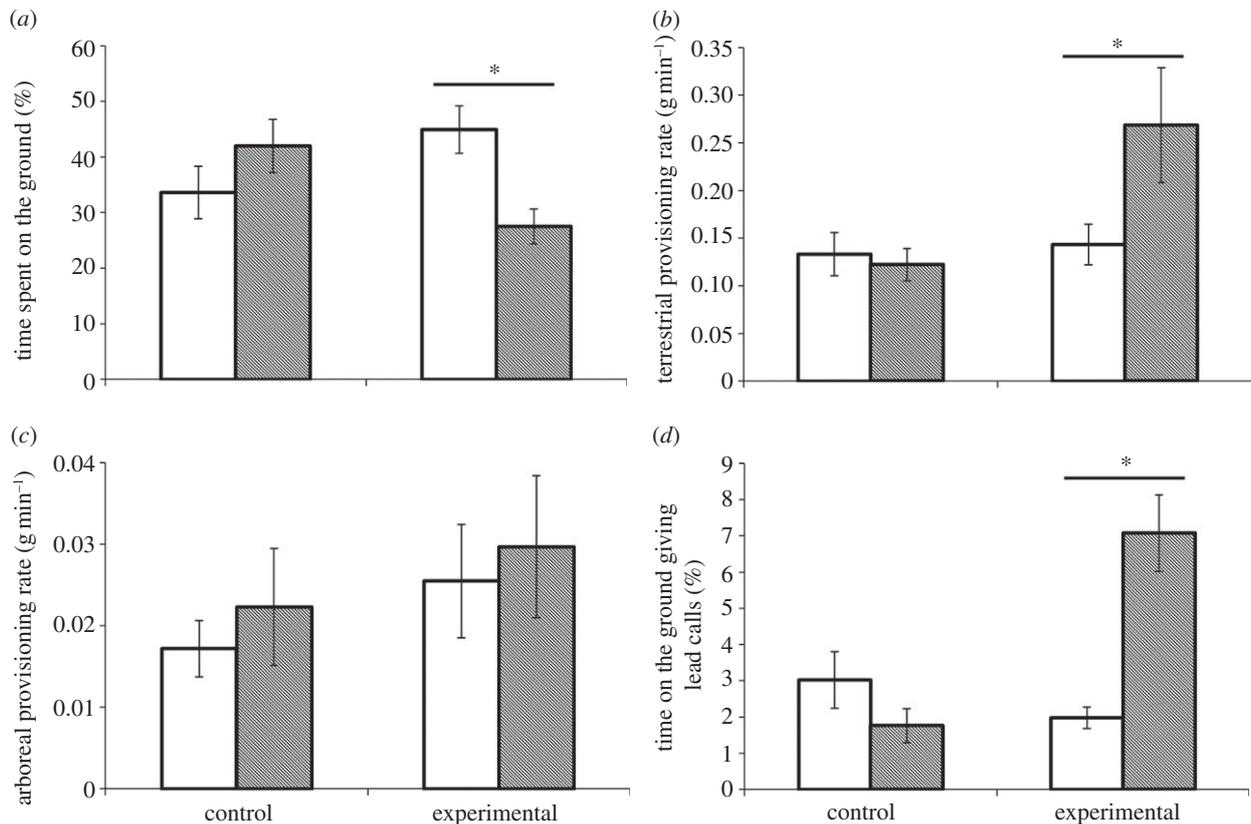
Figure 4. The effect of increasing perceived predation risk on (*a*) time that fledglings spent terrestrially, (*b*) terrestrial provisioning rate (g min^{-1}) to fledglings, (*c*) arboreal provisioning rate (g min^{-1}) to fledglings, and (*d*) percentage of time that adults give lead calls to terrestrial fledglings. All graphs plot means and s.e. Unfilled bars denote 'before' and filled bars denote 'after'.
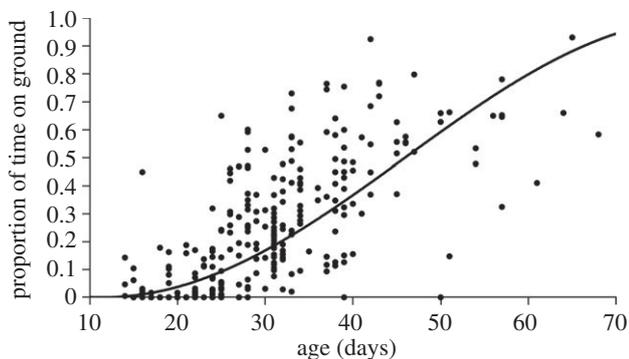
Figure 5. Relationship between fledgling age and fledgling location. Lines show the predictions from the best model investigating proportion of time that fledglings spend on the ground (see the electronic supplementary material, table S6; $n = 309$).

difference in adult provisioning behaviour in relation to fledgling location. If provisioning was solely influenced by proximity, increases in predation risk should have had a uniform effect on provisioning rates. If the increased amount of time fledglings spent in the trees was solely driven by a response to predation risk, adults would not be predicted to alter their provisioning or lead calling behaviour, only fledgling location should change. If provisioning was solely related to fledgling begging levels, then again, no change in provisioning rates would be predicted for increases in predation risk. Finally, if moving to the ground was a signal of quality, adults would not need to alter their behaviour in relation to predation risk, as only fledglings of high enough quality would risk coming to ground. However, following experimental exposure to heterospecific alarms, arboreal provisioning rate remained

constant while carers significantly increased the provisioning and lead calling rates to terrestrially located fledglings. In addition, as fledgling mobility and response to alarm calls improved with age, analogous to being of higher quality, their ability to use moving to the ground as a signal reduces. Hence, these results show that adult provisioning behaviour is only sensitive to changes in perceived predation risk with respect to terrestrially located fledglings. Therefore, our findings support Lummaa *et al.*'s [29] hypotheses: that solicitation displays are more effective at increasing adult provisioning in predator-rich environments.

In this study, we showed a novel way that fledglings can influence the amount of provisioning they received: fledglings can extract more food from adult carers by moving to riskier locations. Different locations (terrestrial and arboreal) have differing predation risk [21], and the mobility of fledglings enables them to use these differences to influence adult provisioning. However, this finding poses one obvious question: why should offspring place themselves at risk? This is particularly relevant as offspring face a permanent cost, death, whereas carers face a smaller cost in terms of lost reproductive success or inclusive fitness [24,38,39]. Hunger has been shown to be a major factor influencing risk tolerance in other species [24,40]. Babbler fledglings seem to show flexibility in their risk-taking, moving to riskier locations when they are hungry but staying in the cover and relative safety of trees when they are satiated. Other species have also been shown to be flexible in their risk-taking, for example, colonies of the ant *Lasius pallitarsis* are willing to forage in high-risk food patches when the pay-offs are higher than those in low-risk patches [41]. As moving to the ground is costlier in terms of predation risk than remaining in the trees,

fledglings may move to a riskier location to signal their hunger to carers [42,43]. In addition, the presence of terrestrially begging fledglings may also increase the predation risk to carers, imposing an additional incentive on adults to provision and thus silence terrestrially located fledglings.

It is likely that the reason fledglings trade-off risk against provisioning is because of the long-term cost of foregoing additional provisioning. In species with high reproductive skew, such as pied babblers [44], the lifetime reproductive cost of not dispersing successfully and/or acquiring a dominant position can be high [45]. As in other species, the amount of care received by pied babblers during early development has long-term effects [46,47]. There is intense competition between same-sex babbler siblings [48], and lower quality offspring are often evicted from the group by their siblings [49]. Evicted individuals risk becoming 'floaters', which carries a significant cost: the longer an individual is a 'floater' the greater their weight loss and the more likely they are to enter a new group as a subordinate [50]. When early condition has such profound long-term impacts, natural selection should favour the evolution of offspring behaviours that gain the greatest amount of provisioning in order to maximize their growth rate. Therefore, adults will increase their provisioning rate to fledglings when they move to the ground in order to encourage them to move back to safety. Larger groups may be able to reduce this conflict as they are able to provision fledglings at higher rates, keeping fledglings closer to satiation and so reducing the benefit they gain from moving to the ground.

The trade-off fledglings face between being fed and avoiding predators is only transient. The dependent phase is dynamic, and as such in a number of species offspring's ability to respond to predation risk improves with age and experience [20,23]. As pied babbler fledglings age, their mobility increases and their response to alarm calls improves. The costs of being on the ground, therefore, decrease with improved fledgling mobility. This is analogous to the 'hide-to-follow' spectrum of young deer [51]: as fawns age, their mobility improves and they transition from 'hiders' to 'followers' in response to predator detection. Therefore, it is likely that as a result of developmental change, babbler adults no longer need to change their provisioning behaviour when fledglings move to the ground. This highlights the fact that the dynamics of offspring–carer interactions are constantly changing owing to offspring development [52].

Being mobile changes the environment for offspring, and the mobility of pied babbler fledglings enables them to use their location in a signalling context. These results add to investigations into the effects of mobility on offspring–carer communication conducted in other species [13,19,53]. For example, the mobile nature of meerkat (*Suricata suricatta*) pups has led to the evolution of multiple begging call types [13,19]. Thus, it seems likely that mobility opens up new avenues for signalling systems.

This study investigates a novel aspect of 'blackmail' by offspring to achieve higher provisioning rates. Our results show that the mobility of offspring, combined with differential predation risks, can be used to influence carers provisioning levels. Mobile offspring may, therefore, be better placed to win the conflict between parents and offspring over provisioning. This study also highlights the fact that POC can take place across multiple developmental stages and can be mediated by more than just begging behaviour, opening up a new avenue of investigation into conflicts and their resolution in animal societies.

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